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THE BLACK SPRUCE (*PICEA MARIANA*) VEGETATION
OF JASPER AND BANFF PARKS

by



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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1971

Thesis
1971 F
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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read,
and recommend to the Faculty of Graduate Studies for
acceptance, a thesis entitled 'The Black Spruce (*Picea*
mariana) Vegetation of Jasper and Banff Parks' submitted by
Ted Fraser Laidlaw in partial fulfilment of the requirements
for the degree of Master of Science.

ABSTRACT

After a preliminary reconnaissance, 16 black spruce stands were selected from Jasper and Banff Parks for intensive study. Emphasis was on wetland vegetation as black spruce is rarely a dominant of the upland soils of the study area. Quantitative vegetational and edaphic data were obtained from each stand.

A Bray and Curtis 2-dimensional stand ordination was constructed solely on the basis of performance of subordinate vascular species, but the relative distribution of stands within the ordination appeared meaningful in overall vegetational and edaphic terms.

A tentative classification of black spruce stands involved the recognition of 4 Groups, corresponding to 4 areas of the ordination:

- 1) The *TOMENTHYPNUM* Group - consists of wooded peatland stands. The dominant peat mosses are *Tomenthypnum nitens* and *Sphagnum* spp.
- 2) The *POTENTILLA* Group - consists of very open stands which have developed on frost-heaved wetland mineral soil.
- 3) The *HYLOCOMIUM* Group - consists of relatively closed black spruce - feathermoss forest (both wetland and upland).
- 4) The MIXED CHARACTER Group - consists of "mosaic" stands having various areal proportions of a number

of relatively homogeneous wetland communities.

The 14 wetland stands have water tables which fluctuate within 1 m of the ground surface. In only one case did peat depth within the peatland stands exceed 1 m.

The substrate is generally very rich in lime. Water samples from wetland stands gave pH's ranging between 6.6 and 8.3, calcium hardness between 80 and 365 ppm, and magnesium hardness between 10 and 95 ppm.

The calcareous substrate has a profound effect on the subordinate vegetation. The stands are species-rich. Many of the vascular species and the dominant peat mosses are known calciphytes. The subordinate vegetation is floristically very similar to that developed on calcareous wetland in the Hudson Bay lowlands.

Fire has predated the establishment of the majority of the incumbent tree-sized black spruce of all stands. Indirect evidence from age structure data suggests that black spruce reproduction by seed on peatland is effective for only a short time following fire, after which vegetative reproduction becomes prominent.

Although lodgepole pine and white spruce, once established, may grow more rapidly than black spruce on wetland, they appear to have difficulty establishing directly on peat mosses.

A comprehensive classification of the wetland vegetation of the Parks would be premature at this time. However, this study indicates that in Jasper and Banff the hydrarch

succession model and the concept of edaphic climax are by themselves inadequate vehicles for the expression of wetland vegetation dynamics. The Fennoscandian wetland terminology framework, used in this thesis and employed with effect elsewhere in North America appears to have considerable value. It is recommended for employment in future studies of western Canadian wetlands.

ACKNOWLEDGEMENTS

I would like to express my appreciation to the following individuals, without whose help this thesis would not have been completed:

1. Dr. G. H. La Roi, for his many valuable ideas and suggestions during the writing of this thesis.

2. Dr. C. D. Bird, University of Calgary, for help in identifying many of the bryophytes.

3. Mr. Mike Ostafichuk, for additional help with bryophyte identification and with soil moisture analysis.

4. Dr. J. G. Packer, for his identification and confirmation of the grasses, rushes and sedges.

5. Miss Madelaine Dumais for her confirmation of the identities of other vascular species.

6. Mr. J. Carlson, of the Agricultural Soil and Feed Testing Laboratory, Edmonton, for analysis of nutrient content of soils.

7. Mrs. K. I. Strausz of the Provincial Water Analysis Laboratory, Edmonton, for analysis of some of the water samples.

8. Mr. Chris Benger, for his excellent field assistance and cheerfulness under sometimes trying circumstances.

9. Mrs. Betty Ford, for her uncanny ability to read my longhand and convert it to print in a most satisfactory manner.

10. Fellow graduate students, Roger Hnatiuk, Julie

Hrapko, John Purchase, Paul Stringer and Arnold Van der Valk for their cheerful company and advice during the writing of the thesis.

11. My wife, Eleanor, for her encouragement and devotion during all stages of research and writing.

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I. RESEARCH OBJECTIVES

The objectives of this study were as follows:

1. To describe the physiognomic, vegetational and floristic attributes of black spruce dominated forest communities in Jasper and Banff Parks.
2. To relate the performance of the subordinate vegetational components of these communities to variation in intensity of selected environmental factors.
3. To relate the dispersion, density, size structure, reproduction and successional relationships of the tree species populations to important biotic and physical environmental factors.
4. To assess the degree of similarity between black spruce-dominated wetland communities in Jasper and Banff Parks to similar communities elsewhere in Alberta and Canada.
5. To provide information that will be of future use in a comprehensive description of the vegetation of the two mountain parks. This study is one of several being carried out within the parks under the guidance of G. H. LaRoi. Objective quantitative sampling techniques were considered necessary to comply with this last objective.

II. SOME RELEVANT CHARACTERISTICS OF BLACK SPRUCE AND ITS HABITAT - A LITERATURE REVIEW

The most comprehensive source of information on the silvics and autecology of black spruce (*Picea mariana* [Mill.] B.S.P.) is A.B. Vincent's literature review (1965). This reference is especially valuable because it contains information from many papers which are difficult to obtain at the University of Alberta.

The list of references in Vincent's review indicates that most of the information on black spruce autecology has been gained from studies in commercial quality stands in eastern Canada and the adjacent United States. Detailed studies of black spruce stands in western and northern Canada have begun only recently. A comprehensive description of black spruce forests in the foothills of western Alberta (Edson-Hinton area) is provided by Horton and Lees (1961).

A. Geographic Range, Races, Hybrids

The botanical range of black spruce is very large. Together with that of white spruce (*Picea glauca*) the range coincides with the distribution of the boreal taiga zone in North America and its transitions to adjoining zones south and west. The species is found in all Provinces of Canada, the Northwest Territories, Yukon, Alaska and the northeastern United States from Maine to Minnesota. In northern Canada the range limit generally coincides with the tree line (Heinselman 1957; Larsen 1965; Vincent 1965).

The species occupies the northern two-thirds of the

Province of Alberta. In Alberta, its range dips furthest south in the mountains, terminating near the origin of the South Saskatchewan River in northern Banff Park. The southern border of its range then passes in a northwest direction through interior British Columbia and into Alaska (Heinselman 1957).

There are no taxonomically recognized varieties of black spruce. Heinselman (1957) states, however, that the existence of geographic races in black spruce is considered likely by many forest geneticists. The presence of "upland" and "lowland" ecotypes is also considered possible.

Introgressive hybridization, resulting in large hybrid swarms, is frequent between black spruce and red spruce (*Picea rubens*) where their ranges overlap in eastern Canada and New England (Morgenstern and Farrar 1965).

Natural hybrids between black spruce and white spruce are apparently rare, although a few isolated reports are mentioned by Vincent and Heinselman. Larsen (1965), working in the forest-tundra ecotone of the central Northwest Territories, found morphological intermediates between black spruce and white spruce to be common on a large esker.

B. Gross Morphology of Mature Trees

The root system of black spruce is typically very shallow and platelike. Maximum depth of root penetration is

rarely more than 60 cm and they are usually confined to the upper 15 to 30 cm regardless of whether the soil is mineral or organic. The radius of the root system may be as great as 9 m (Anon. 1961; Heinselman 1957; Horton and Lees 1961; Vincent 1965).

Black spruce has the ability to form adventitious roots when paludification occurs due to rising levels of moss. Vincent notes that this largely accounts for the adaptability of black spruce to wetland conditions. As many as five successive layers of adventitious roots have been recorded (Le Barron 1945).

The largest dimensions recorded are a height of 31 m with a diameter of 91 cm (Anon. 1961; Sargent 1898) but individuals of such size must be very rare. Heinselman states that over much of the commercial range average pulpwood stands run about 12 to 25 cm DBH (diameter at breast height = 1.5 m). On very extreme sites, however, it may not be larger than a tall shrub at maturity and in the north may have the appearance of a semi-prostrate mat at the limit of its range.

C. Reproduction

The seed cones of black spruce are produced near the top of the stem. In open stands they may first appear when the tree is only 15 years old (Horton and Lees 1961). I have often observed cone-bearing individuals less than 1.5 m tall in the course of this research. Peak cone production occurs about every 4 or 5 years (Heinselman 1957; Blais 1957).

The cones of black spruce are semi-serotinous, releasing their seed at a fairly steady rate over a number of months. They remain on the trunk for a variable length of time - up to 60 years according to Hustich (1965), but usually less than 30 years (Heinselman 1957; Vincent 1965). Seed viability decreases fairly rapidly within 5 years of maturation but small quantities of viable seed have been collected from cones as old as 15 years (Chai and Hansen 1952).

The above-mentioned facts ensure that a continuous seed supply is present in stands which have reached cone-bearing age. Black spruce's reputation as a "fire species" is explained by this and also by the fact that viable seed often remains on the tree following fires so intense that the tree itself is killed.

The seeds of black spruce are small, winged and light, but wind dispersal of the seeds is apparently not very efficient. Seed catch trials in eastern Canada and the adjacent United States have indicated that seed fallout is practically nil at distances greater than a few tree lengths downwind of the stand (Vincent 1965). Seed falling in winter, however, can undoubtedly travel much greater distances over ice or glazed snow.

Black spruce regeneration is very much affected by seedbed quality as the young seedling is quite delicate and especially prone to death by drought, heat, or smothering by actively growing moss. It is probably dangerous to generalize about the suitability of the various seedbeds

available to black spruce without geographic qualification. Le Barron (1944) working in relatively dry upland stands in Minnesota, found that bare mineral soil was a better seedbed than litter, burned duff or scarified shaded duff. Johnson (1956) also found mineral soil superior to undisturbed humus. Linteau (1957) studied disturbed upland sites in Quebec and found that stocking to black spruce seedlings was significantly more frequent on soil colonized by *Polytrichum commune* and *P. juniperinum* than on bare sandy soils. The *Polytrichum* may improve the moisture characteristics of the soil surface or possibly it is a good indicator of otherwise favourable seedbeds. It is generally held that "feather-moss" carpets provide a very poor medium for seedling establishment (Horton and Lees 1961; Hustich 1965; Vincent 1965). Vincent notes, however, that the earlier stages in the development of a feathermoss mat are superior to the needle litter carpet which precedes these stages on upland sites.

Sphagnum mosses vary considerably in their seedbed characteristics and the literature is somewhat contradictory. Both Heinselman (1957) and Vincent (1965) conclude that the slow-growing species of *Sphagnum* provide a good medium for germination and establishment while the rapidly growing species tend to smother the seedlings.

Exposed fire-blackened surfaces tend to be poor seedbeds as they often develop temperatures which are lethal to the seedlings (Le Barron 1944). Because of this the near simultaneous occupation of a fire-blackened soil surface by

lodgepole pine (*Pinus contorta*) or jackpine (*P. banksiana*) and black spruce may be of benefit to the latter species. Pine seedlings can apparently withstand higher soil temperatures than black spruce and the pine foliage may ameliorate the microclimate to the point where successful establishment of black spruce is possible.

Black spruce is well-known for its ability to reproduce vegetatively. "Layers" are formed when drooping branches come in contact with and are enveloped by, rising moss - generally feathermoss or species of *Sphagnum*. The branch in time sprouts roots, develops apical dominance and an erect form. Eventually its contact with the parent tree is lost. In many stands characterized by the rank growth of moss, layering is virtually the only means of reproduction available to black spruce. Competing species without this means of reproduction (e.g. *Picea glauca*, *Pinus banksiana*, *Pinus contorta*) often cannot persist.

Mature trees originating from layers may usually be recognized by their arcuate trunk bases, although these may be mostly buried in moss.

Le Blanc (1955) has reported a phenomenon termed "rooting" in Quebec. The superficial roots of black spruce turn upward and produce normal shoots. Rootings and layers may be difficult to distinguish from each other in the field. Horton and Lees (1961) reported rootings to be abundant in the Alberta foothills, but further examination by them at a later date revealed that most of the "rootings" were, in fact, layers (Vincent 1965).

D. Biotic Factors Responsible for Deformation and Death of
Black Spruce

In eastern Canada and the adjacent United States the most serious parasite of black spruce is dwarf mistletoe (*Arceuthobium pusillum* Pk.), a parasitic angiosperm which causes "witches broom" and associated stunting of growth and eventual death (Vincent 1965). *A. pusillum* has not as yet been reported in Alberta, but "witches broom" caused by the systemic rust *Chrysomyxa arctostaphyli* Diet. is common (R.A. Blauel*, personal communication).

Spruce budworm (*Choristoneura fumiferana* Clem) can cause serious defoliation of black spruce in stands where black spruce is mixed with the preferred food (*Abies* spp., *Picea glauca*). Pure stands of black spruce are usually not damaged (Blais 1957).

Vincent (1965) notes that black spruce is much less affected by heart rot than any other major tree species in Canada. Black spruce is not a preferred food of any mammal common to upland or wetland stands. Occasionally, during periods of peak abundance, snowshoe hares (*Lepus americanus*) will do considerable damage to the leaders and branches of seedlings (Heinselman 1957). The cone-gathering activities of the red squirrel (*Tamiascurus hudsonicus*) are apparently responsible for the club-shaped top common to black spruce. Beaver (*Castor canadensis*) do not feed on black spruce but

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PLATE I. A black spruce tree exhibiting crown mutilation by red squirrel and "witches broom" caused by the rust *Chrysomyxa arctostaphyli*.

may indirectly cause the death of many trees due to flooding.

Commensalistic lichens (*Usnea* spp., and *Alectoria* spp.) commonly festoon the branches of black spruce - occasionally to a very marked degree. I believe it possible that these festoons could adversely affect the growth of the tree by considerably decreasing the intensity of light reaching the middle and lower branches. As far as I know, however, research has not as yet been applied to this question.

E. Habitat, Seral Characteristics

A detailed description of the range of habitats occupied by black spruce is beyond the scope of this review. The following account is therefore highly generalized and slanted towards the objectives and findings of my research.

Black spruce apparently has a broad ecological amplitude. North American foresters generally divide its habitats into two broad categories - "upland" and "lowland". The latter term is perhaps unfortunate, as it has relatively little edaphic significance in mountainous areas. The terms "wetland", "peatland", "mire" etc., are more appropriate.

Throughout its range black spruce is most frequently found on organic terrain characterized by varying degrees of wetness. A common associate on such terrain (east of the Rocky Mountains) is tamarack (*Larix laricina*). Over the southern portion of its range in the United States and the Prairie Provinces, black spruce is largely restricted to such soils where it may form a physiographic climax or part of a wetland climax cycle (Heinselman 1963). Organic terrain

varies greatly, even on a local scale, in nutrient status, physiography and vegetation. This has led to problems in terminology and classification regarding this type of terrain and its associated vegetation. Sjörs *et al.* (1965) sum up the situation as follows:

"Mires, being hybrids of both, are variable to a much greater extent than any kind of true terrestrial or true aquatic vegetation. ...it has been possible in Sweden... to obtain a broad picture of the chief communities in many other kinds of vegetation and even to carry out their investigation in considerable detail. But regarding mires this has been possible only for special types such as the bogs, or for narrowly delimited districts. It is not permissible to extrapolate very far from this limited experience, every new mire area investigated showing large deviations from expected vegetational composition and structure.

The reasons for this dilemma are the marked reciprocity of the relations between habitat conditions and vegetation in a mire, the locally divergent successional trends, and finally the close dependence of a mire on local conditions such as relief, hydrology and types of subjacent and adjacent mineral deposits. The widespread occurrence of structural surface patterns...in the Boreal mires (northern coniferous and subalpine belts) further complicates the picture, for these patterns are ever-changing and still not well understood."

Ritchie (1960b) emphasizes that peatland researchers in North America should apply northern European terminology and

classification systems wherever possible. Their literature is much more extensive than our own and the physiographic and vegetational similarities of peatlands in the two areas are remarkable - differences being of a minor floristic nature.

One useful method of describing peatland, which is commonly incorporated into various Swedish and Finnish classification systems, is in terms of nutrient regime. At one end of the spectrum are "bogs", characterized by very poor nutrient status, highly acidic soil water (low pH) and associated extreme forms of vegetation. Species diversity is generally low and many of the vascular species belong to the ericaceous group. Various species of *Sphagnum*, largely responsible for the acidity, dominate the moss carpet. The surface of the bog receives few nutrients from below or laterally. "Ombrotrophic bogs", the most extreme form, receive most of their nutrients through precipitation and dust fall-out (Sjörs 1961).

At the opposite end of the spectrum, in terms of vegetation, are the "rich fens", which occupy "minerotrophic" peatland. This type of peatland is generally characterized by a soil water rich in cations, particularly calcium and magnesium. This results in a relatively high pH. Definitive statements about pH ranges cannot be made, however, as a given pH is the net result of the interaction between peat (and living acid-forming *Sphagnum*) and the cation-rich water. Rich fens have a much greater species diversity than bogs and calcicolous

species tend to be abundant. Rich fen develops on substrates rich in lime or penetrated by streams which have passed through such deposits. Sjörs (1961) also recognizes "moderately rich", "intermediate", and "poor" fens - the latter type much resembling a true bog. In fact, a complete continuum of vegetation and degree of eutrophy appears to exist between the ombrotrophic bog at one extreme and rich fen at the other.

Bogs and fens may be separated by distances of only a few meters, reflecting local groundwater conditions (Sjörs 1961).

"Muskeg" is peatland (either ombrotrophic or minerotrophic, according to Sjörs (1961)) which is occupied by stunted, well-spaced trees.

Black spruce is commonly found in the bogs of North America and it is becoming apparent that it is a dominant of the drier types of minerotrophic peatland as well (Sjörs 1961). On both wetland types it is frequently accompanied by tamarack (*Larix laricina*) which tends to become more prevalent with increasing minerotrophy, commonly being found as the sole dominant in "larch fens" (Ritchie 1960a, 1960b; Sjörs 1963).

Horton and Lees (1961) note the absence of "typical acid bogs" from the lower foothills of Alberta and comment on the frequency of "high pH" (calcareous) peatland in the foothills. The lowest pH of any peatland studied in the foothills was 5.5, while calcareous peatland from the upper foothills gave values as high as 8.0. Black spruce appeared to grow as well on the calcareous as on the weakly acidic peat.

Thus far I have been dealing with the wetter end of the soil moisture spectrum occupied by black spruce. This species is also a frequent component of moist-to-mesic upland forest, occupying mineral soil of a wide textural range. On moist clayey and loamy uplands of the boreal forest the most frequent codominants are white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), paper birch (*Betula papyrifera*) and tamarack (*Larix laricina*). On more sandy and dry soils jack pine (*Pinus banksiana*) is the usual associate in the eastern half of its range (Heinselman 1957). Further west, jackpine is replaced by the ecologically-similar lodgepole pine (*Pinus contorta*) which is common on moist loamy soils as well as dry sandy soils. This pine is also commonly found on wet organic terrain in western British Columbia, where black spruce does not occur.

An abundance of black spruce on upland sites can usually be traced to fire. Following intense fire, varying amounts of black spruce, poplar, white spruce, paper birch and pine may enter the site, relative amounts depending on the nature of the seedbed, proximity of seed sources and the abundance of poplar in the pre-fire forest. All of these associated species usually grow faster than black spruce, so initially this species is present as an understory where the other species are present.

However, black spruce is moderately shade-tolerant and long-lived relative to the pine and poplar species, and thus can eventually succeed them. Its ability to reproduce vegetatively is also of advantage and if fire disturbance

does not interrupt this trend, black spruce (often with some white spruce) will achieve dominance on the site, the result being an even-aged stand so typical of upland black spruce (Vincent 1965). If the stand is dense and dark, black spruce may not regenerate beneath its own canopy, either vegetatively or by seed. Reproductive size classes may then be usurped by balsam fir (*Abies balsamea*) or subalpine fir (*Abies lasiocarpa*) which are more shade-tolerant and reproduce prolifically by layering. Alternatively, the stand may break up with advanced age, allowing regeneration of black spruce and resulting in an uneven age structure. Such uneven-aged upland black spruce stands are apparently rare, owing to the frequency of fire in the boreal forest (Vincent 1965).

In western Alberta it is common to see older upland fire-origin lodgepole pine stands being gradually invaded by black spruce from adjacent peatland. As the peatland supports an open type of forest, there are usually always cone-bearing black spruce present, even if the stand is very young (15-30 years). However, on upland sites, understory black spruce may not produce seed cones until they are much older. A fire occurring before sexual maturity will tend to wipe out the upland black spruce population. The same fire passing through the peatland may remove the incumbent population of black spruce, but seed-fallout will quickly re-establish it. Also, peatland forest is less prone to complete destruction due to its open nature.

The result is that peatland often provides a "refugium" for black spruce, from which it can migrate and colonize

adjacent uplands. The significance of these refugia increases with the frequency of fire.

III. PRELIMINARY RECONNAISSANCE

A preliminary reconnaissance of Jasper and Banff Parks was made in September, 1966 and May, 1967. Aerial photographs (scale 1:40,000; 1949-52) of the parks were studied before entering the field, but considerable difficulty was experienced in locating black spruce stands by this technique. Wetland black spruce stands were practically indistinguishable from poor quality wetland white spruce stands, which seem to be abundant in the lowlands of the two parks. These latter communities merit further attention - the white spruce have a morphology very similar to peatland black spruce and the physiognomy of these communities is similar to the muskeg type usually associated with black spruce.

Because of this problem, the reconnaissance largely involved cruising the highways and accessible back roads of the two parks in search of black spruce.

In Jasper and northern Banff black spruce is a frequent occupant of upland and wetland sites within the montane and lower subalpine zones, but is rarely very abundant in any one location. In neither park was the species found at elevations greater than approximately 2,000 m (6100 ft), although extensive observations at such high altitudes were not made.

Although black spruce seems to grow well on well-drained upland soil of glacial origin, it rarely forms pure stands or achieves numerical dominance on such sites. Usually it is overtopped and outnumbered by lodgepole pine of fire origin. Frequent associates in the understory are white and Engelmann

spruce (*Picea engelmannii*), the latter becoming more abundant with increasing altitude. Subalpine fir may also be present. A number of pine forests were seen, however, in which black spruce was the sole tree species in the understory. It appears probable that, barring fire, these sites will in future be occupied by relatively pure stands of black spruce.

At present, relatively pure stands of black spruce are largely restricted to wetland sites. Such areas are generally small in size but fairly common in shallow depressions and drainage channels linking lakes, etc., in the bottoms of the major valleys. They are also not uncommon below seepages on the valley slopes and in the form of narrow bands along small meandering streams coursing down through other vegetation types on gentle upland slopes. The term "lowland" and "wetland" are not synonymous within the parks.

Tamarack (*Larix laricina*), a common wetland associate of black spruce in the foothills adjacent to Jasper, is evidently very rare; one very small population was seen along the Miette Hot Springs Road in the eastern portion of the park. White spruce is a frequent associate of black spruce on wetland sites in the parks and, more rarely, lodgepole pine is present as well.

The reconnaissance quickly established that most of the low-elevational wetlands in Jasper and northern Banff are rich in marl deposits. The pH of the water in the peatlands and streams ranges from 6 to 9. This is due to the abundance of limestone and dolomite rock strata and subsequent calcareous nature of much of the glacial drift in the parks.

Areas of homogeneous vegetation and physiography are

usually very small in the wetlands; slight changes in relief give rise to vegetation of very different nature. In short, vegetation-edaphic-topographic relationships are very sensitive and complex in the wetland habitats of the study region.

IV. SAMPLING CRITERIA

Sampling criteria were of necessity loose and somewhat flexible. It was realized following the Preliminary Reconnaissance that sampling criteria could not be too stringent, or the number of stands acceptable would be too few.

A "black spruce-stand" was defined as a tree-dominated plant community in which individuals of black spruce greater than 2.5 cm DBH accounted for at least 50% of the tree density. The 2.5 cm lower limit was necessary because of the very slow growth and resultant small size of black spruce on many sites numerically dominated by it.

Wide ranges of tree density were acceptable to insure that a full and unbiased range of canopy closures would be included in the study.

In order to be sampled, a stand had to exhibit a certain amount of "homogeneity", the term being used in the following manner. In general, a stand was considered homogeneous if whatever discontinuities present (e.g. clumps of trees, hummocks and hollows) repeated themselves throughout the stand. Gradients were acceptable provided they were not too steep and did not include very marked discontinuities.

It is often difficult, within the parks, to establish the degree of human disturbance to a site. However, stands were omitted from selection if there was any indication of direct human interference in the form of axe marks, hiking trails, etc. Many of the black spruce stands selected are, however, located near roads or highways, for obvious logistical reasons.

V. METHODS

Each "stand" was a 50 x 20 m rectangle, centrally located in a study area which met the sampling criteria (Fig. 1). This rectangle was divided into five 20 x 10 m rectangles. In each of these the following sampling techniques were employed and data obtained:

1. Four 5 x 5 m quadrats were randomly selected from the eight in each rectangle. In each quadrat the DBH's of all woody stems were measured with Swedish diameter calipers. Two stems, irrespective of species, having a DBH of at least 2.5 cm were objectively chosen from each quadrat for measurements of height, diameter and age. Increment cores were taken at "stump height" (30 cm) with a "Djos" increment borer. Ages were determined in the laboratory with the aid of a binocular microscope, the cores first being prepared with a lignin stain (Phloroglucinol + a few drops of concentrated HCl). Staining was necessary because the growth rings of black spruce were often very narrow. Tree heights were measured with a Blume-Leiss altimeter.

Additional trees were sometimes selected for the above measurements - to provide further insight into stand history, or because the individual was the largest of its species within the stand.

Basal areas of the tree species were estimated with a Bitterlich prism from the centre of each quadrat.

2. Ten 2 x 2 m quadrats were randomly chosen from the 50 in each rectangle (see Fig. 2). Each was sampled for the density of stems of tree species of height 30 cm to 1.5 m.

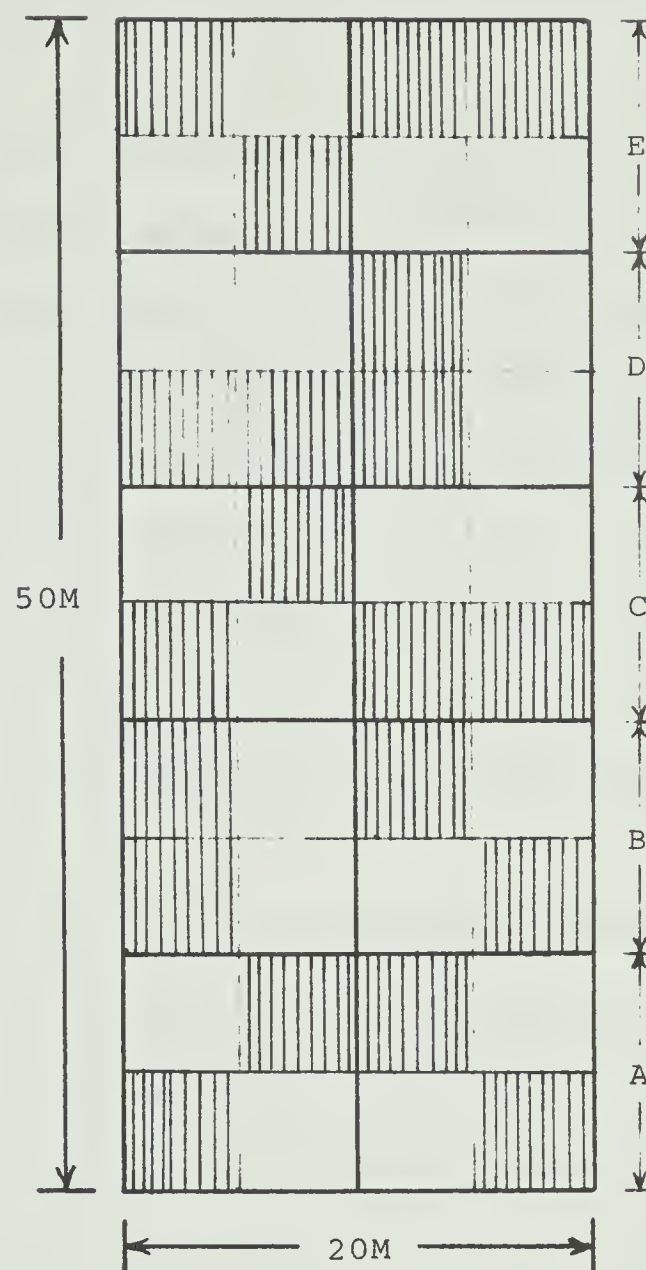


FIGURE 1. The 5x5 M sampling plan used in obtaining mensurational data. Four quadrats were selected from each of Blocks A, B, C, D, and E.

This reproductive size class will be referred to as "transgressives".

3. A 1 x 1 m quadrat was nested within each 2 x 2 m quadrat. Each was sampled for the presence of the shrub and herb species and density of tree seedlings. The term "seedling" refers to individuals of the various tree species less than or equal to 30 cm in height. No distinction was made between "seedlings" of seed and vegetative origin.

A moss and lichen sample was collected from a specified corner of each 1 x 1 m quadrat. This was later analyzed in the laboratory for the presence of the less common moss and lichen species.

4. A line of 100 vertical cover points was located at 20 cm intervals along the long axis of each rectangle. At each point, cover was determined with a #14 knitting needle passed vertically downward through the lesser strata of vegetation. The presence or absence of species of subdominant strata and of tree foliage above or below each of the points were recorded.

All vascular species found inside the 20 x 50 m stand were recorded on a Constance List, irrespective of whether they had been noted in quantitative sampling. Voucher specimens were collected of species of uncertain identity. These specimens have been deposited in the Herbarium of the Department of Botany, University of Alberta.

The slope of the stand was measured with an Abney level from the centre of the stand.

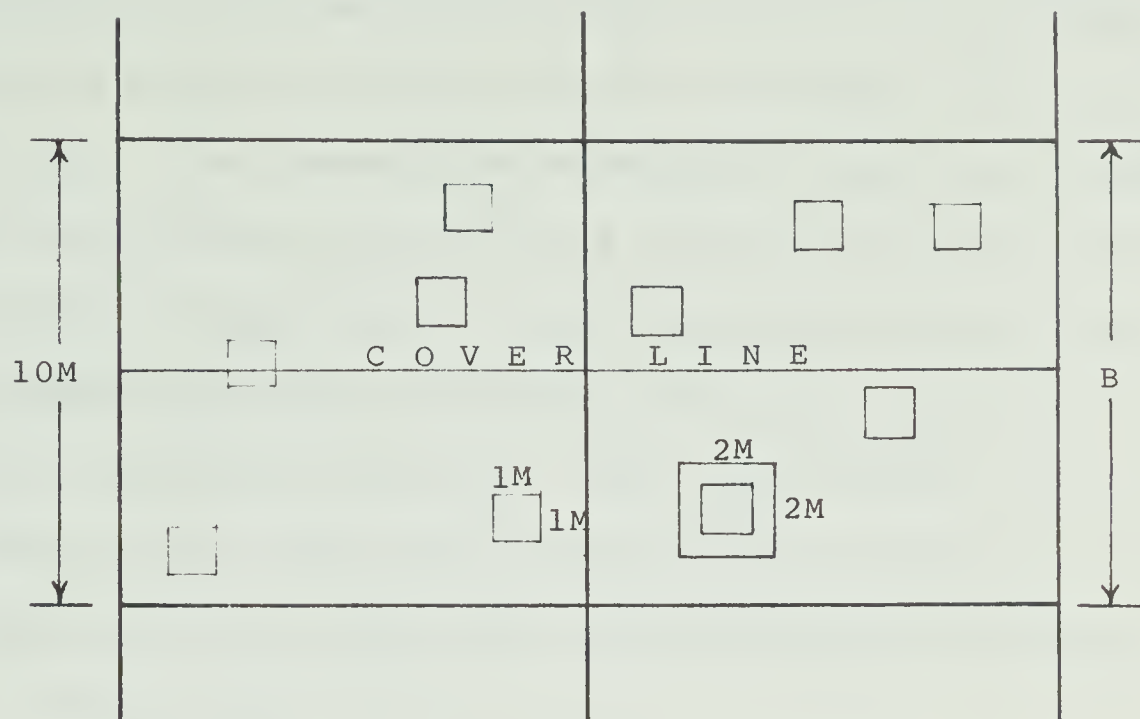


FIGURE 2. The 1x1 M, 2x2 M quadrat sampling plan. Ten 2x2 M quadrats were selected from each of Blocks A to E. A 1x1 M quadrat was nested within each. Also shown is one of the 5 Cover-lines used in obtaining vertical cover data.

A soil pit of at least 45 cm depth (usually more) was excavated in a central location within the stand and the profile described. Soil samples were collected from the horizons recognized, air-dried, ground with a mortar and pestle and sieved through a 2 mm screen. The Alberta Government Soil and Feed Testing Laboratory in Edmonton tested the 2 mm fraction for available nutrients. The 2 mm fraction of mineral horizons was subjected to mechanical analysis for percent sand, silt and clay using the hydrometer technique outlined in Bouyoucous (1951).

A water sample was collected from the soil pit after suspended solids had been given time to settle out. This sample was tested in the field for calcium and magnesium hardness, phosphate, and nitrate, using a Hach Model DREL water analysis kit. The pH was determined with a Metrohm Model E 280 portable pH meter with glass electrode. In Stands 11 and 13 the soil pit did not penetrate to the water table, and water samples were, therefore, not taken from the pit. A small stream ran alongside Stand 11 and a water sample was taken from this; presumably it represents the ground water of the immediate area. No sample was obtained from Stand 13.

In the last two weeks of July, 1968, the 14 stands studied in 1967 were re-visited and water samples were again collected from the soil pits. A water sample was not taken from Stand 6 as the soil pit had filled in. Samples were analyzed for total hardness by the Provincial Water Analysis Laboratory in Edmonton. Stands 15 and 16 were first studied

in 1968; they were thus not field analyzed with the Hach kit.

In July of 1968, 20 soil samples were randomly selected from each stand. At each sampling point the living moss layer was removed and a 15 cm vertical core of soil was removed with a peat borer of diameter 2 cm. Each core was weighed shortly after collection and then air-dried. The cores were then oven-dried at 105°C in Edmonton and the weights recorded. Following this, the 20 cores were pooled and mixed to form one sample representative of the stand. This sample was ground with a mortar and pestle and passed through a 2 mm sieve. Part of the 2mm fraction was analyzed for nutrients. If the combined sample was predominantly mineral another fraction was subjected to mechanical analysis. A third part was tested for moisture retention characteristics. The amounts of water held at "Permanent Wilting Point" (15 atmospheres) and "Field Capacity" (1/3 atmosphere) were determined with the use of Soil-test Ceramic Plate Extractors (Models #1500 and 1600).

From this information, pertinent aspects of the soil moisture regime of the surficial soil horizons of the stands were obtained. Total Water Content (TWC) is the amount of water present in the soil at the time of sampling. Total Water Content has three components:

- 1) Excess Water (EW) which is often referred to as "gravitational" water, is the portion of TWC which is held at tension less than 1/3 atmosphere. Large amounts generally are associated with poor soil drainage and consequent poor aeration.
- 2) Biologically Available Water (BAW). This is the

amount of water held between 1/3 atm. and 15 atm. tension. The amount that can be held is a measure of a soil's resistance to drought. When there is abundant Excess Water, BAW tends to lose its biological significance.

- 3) High Tension Water (HTW). This is the portion of TWC which is held at tension greater than 15 atm. but which can be removed by oven drying at 105°C for at least 24 hours. It has little ecological significance but may comprise a large proportion of TWC in organic and heavy mineral soils.

All the above quantities will be expressed on a unit volume basis as gms per 100 cc core volume*. The surface soil horizons of the various stands differ so greatly in bulk density that comparisons of soil moisture regime on a weight basis would be less meaningful ecologically. This has been demonstrated for soil nutrients in black spruce forest soils of Alaska by Heilman (1966).

* "Soil Moisture Density" = gms H₂O/100 cc soil volume.

VI. STAND LOCATIONS

During the summer of 1967 and part of that of 1968, a total of 16 stands were sampled - 14 in Jasper Park and 2 in Banff. The stands have been numbered from 1 to 16 according to sampling date sequence, Stand 1 being the first studied and Stand 16 the last.

The map locations of the stands are presented in Figure 3. Exact map coordinates, altitudes, locations relative to prominent local geographic features, sketch descriptions of surrounding vegetation and sampling dates are presented below. The sampling periods given are those in which all quantitative vegetation analysis took place.

Stands which are located in very close proximity to each other are grouped together in the following discussion.

Stand 1 Jasper 117°54'; 52°41' Alt.= 1204 m (3950 ft)
June 14 - 19, 1967.

This stand is located at the south end of a small, nearly unnamed lake situated approximately 2 km southeast of Leach Lake, in the bottom of the Athabasca River valley. On its north side, the stand is bordered by a partially floating sedge mat extending out into the lake. A narrow stream which connects the lake to a series of smaller lakes to the south bounds the stand on its west side. On the east and south Stand 1 is bordered by slopes of glacial drift occupied by lodgepole pine forest with a scattered understory of black spruce, white spruce and subalpine fir. The dominant shrub on these treed slopes is *Shepherdia canadensis*, an

indicator of mesic to somewhat dry soil. The stand itself is on a small shelf of flat land which links the slopes to the shoreward edge of the sedge mat. The change between the vegetation of the stand and that of its surroundings is very abrupt.

Stands 2, 3, 4 Jasper 118°06'; 53°00' Alt.= 1006 m (3300 ft)

June 26 - July 7, 1967

These stands are located about 2.5 km northwest of Henry House, about 0.5 km southwest of the Snaring River campground and near the confluence of the Snaring and Athabasca Rivers. They occupy a peculiar type of landform which appears from aerial photos to be a former delta of the Snaring River. This "delta" has a slight slope to the SE. The upstream, or NW end has abundant gravelly deposits and is occupied by a dry lodgepole pine forest. An occasional large Douglas fir (*Pseudotsuga menziesii*) towers above the pine and some black and white spruce are also present.

Bordering this pine forest on the south and east is a band of heavy mineral soil which is very sparsely populated by stunted black spruce and white spruce and, more rarely, pine. The soil has been thrown up into hummocks by frost action - a process which is still active. Stand 2 is located in a portion of this belt which is locally dominated by black spruce (see Plate II, Photo 2).

Yet further to the south and east is a large band pocked by numerous large depressions, which though shallow are very well defined (see Plate II, Photo 1). They are

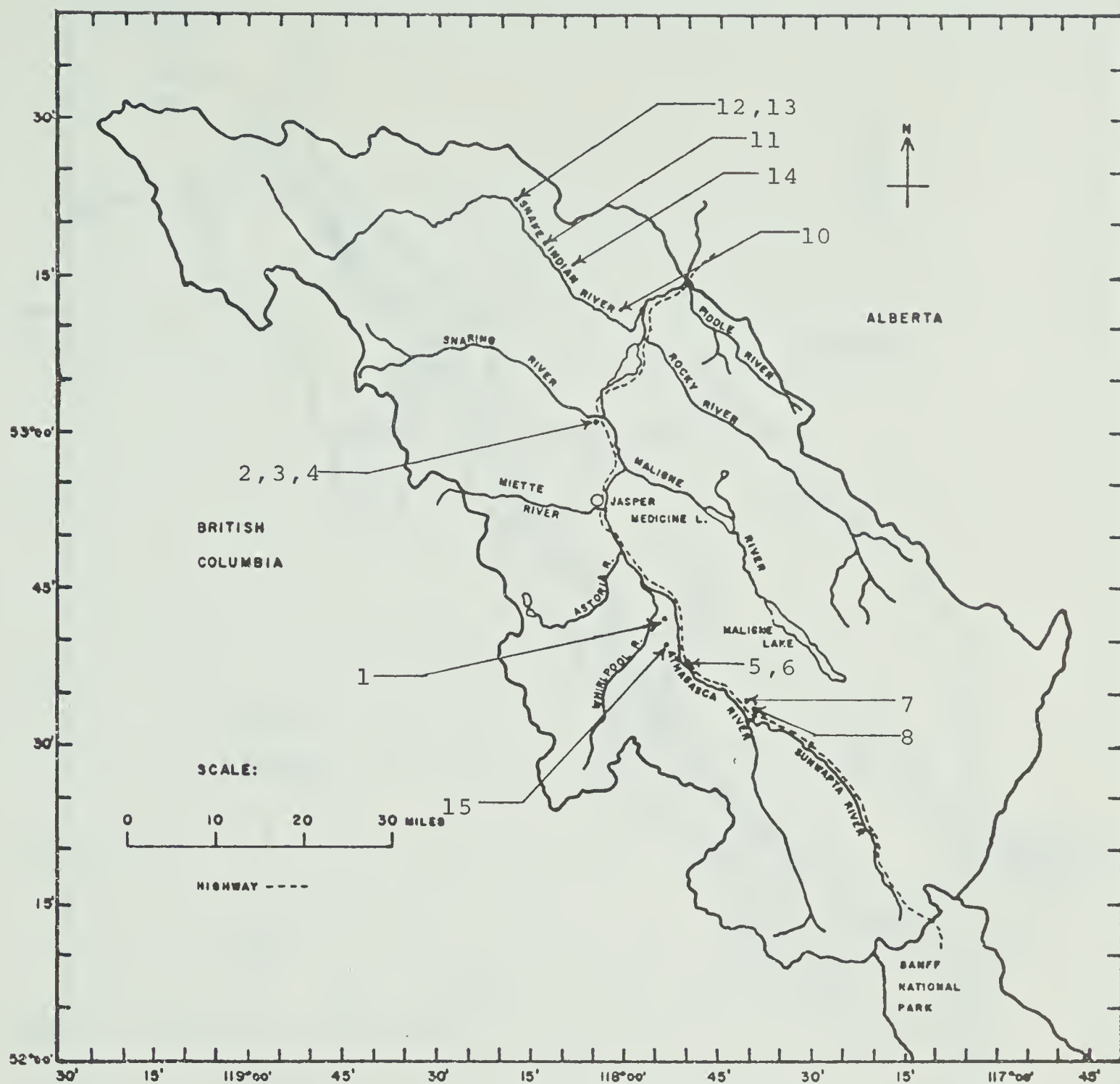


FIGURE 3. *Maps of Jasper and Banff Parks Showing Locations of Stands.

a) Jasper Park

* - Map outlines from Beil (1966).

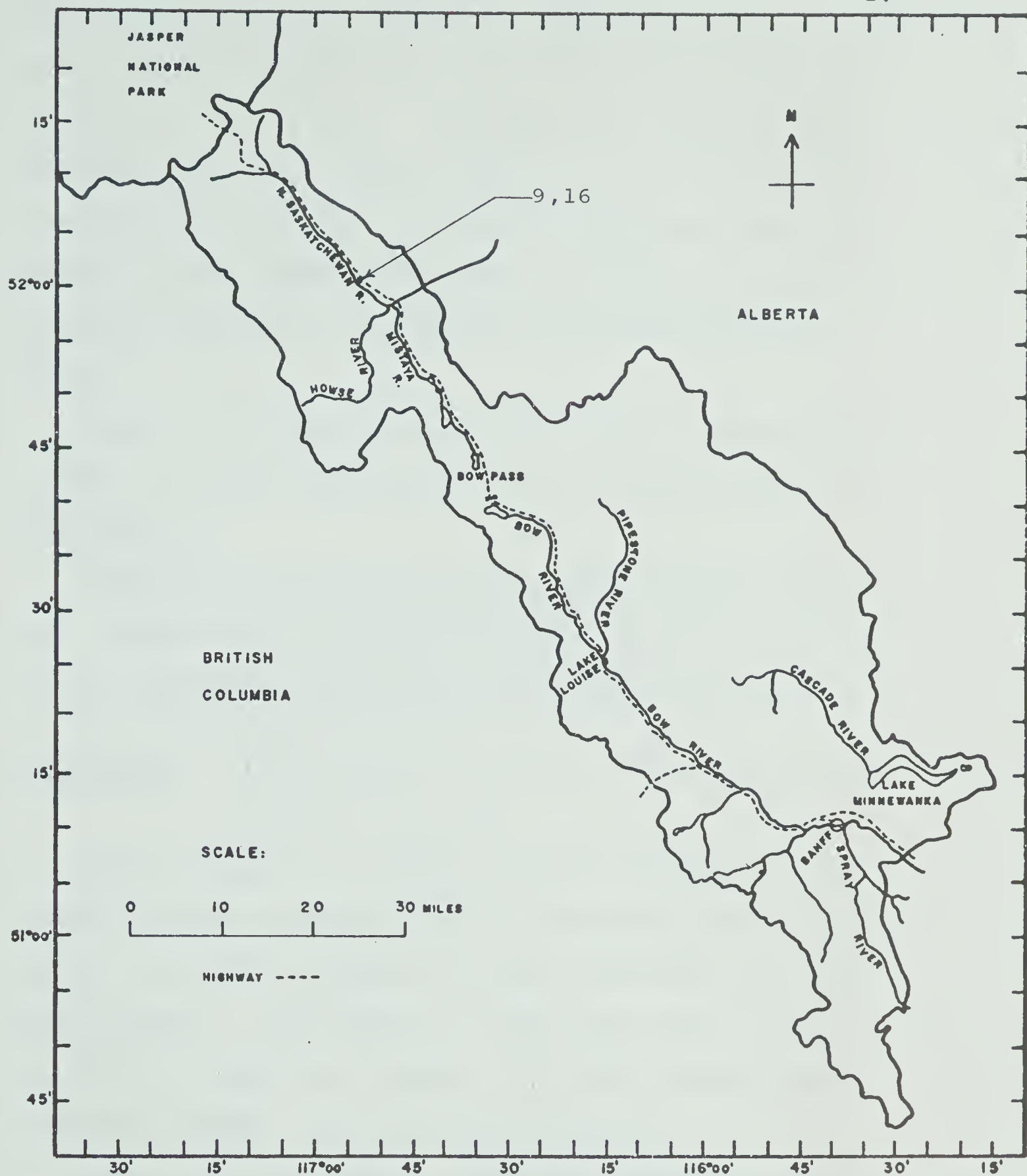


FIGURE 3. Cont'd.

b) Banff Park

flat-bottomed and vary from 25 to about 200 m across. Some contain up to 0.5 m of water in the spring but they may be quite dry by late summer. The water has a high pH (spot readings gave values ranging from 7.5 to 9.5) and crusts of white salts form on the depression bottoms during dry periods. These depressions appear to have been formed by localized upwelling of groundwater passing beneath the "delta".

Stand 3 is located in this band, and is surrounded by a number of these depressions. It is situated about 75 m from Stand 2.

Stand 4 is located alongside a small shallow stream (10 m across) which borders the south side of the "delta". Stands 3 and 4 are separated by a distance of about 75 m.

Stands 5, 6 Jasper 117°51'; 52°37' Alt.= 1234 m (4050 ft)
July 8 - 16, 1967

These 2 stands are located in the bottom of a small drainage channel emptying into the Athabasca River, approximately 6 km SSE of Athabasca Falls, alongside the Jasper-Banff highway. The channel is only about 100 m across and is now largely filled with muskeg. A narrow shallow stream drains the channel (see Plate III, Photo 1).

Stand 5 is a wet muskeg community, representative of much of the vegetation in the channel. Stand 6 is completely different, although it is situated only 40 m from Stand 5. In physiography and vegetation it bears a great resemblance to Stand 2. The slopes adjacent to the channel are dominated



PLATE II

Photo 1. Wetland area dominated by black spruce in vicinity of Snaring River campground, Jasper Park (looking north from the Palisades).

In the background is a stand of lodgepole pine which borders the Snaring River. On the south, the pine is bordered by tall white spruce. The bottom two-thirds of the photo is dominated by black spruce. Frost-heaving is common in the area south of the pine. Note the large depressions in the lower right corner of the photo. These usually contain water but the summer of 1967 was very dry - white crusts of carbonate cover the surface of most of the depressions.

Most of the black spruce dates from a fire of 110 years ago. Note the variation in size of the black spruce, reflecting edaphic conditions.

Photo 2. The interior of Stand 2.

Note the frost-heaved mineral substrate and the trail beaten by ungulates.

by upland pine-spruce forest.

Stand 7 Jasper 117°40'; 52°33' Alt.= 1402 m (4600 ft)
 July 25 - 27, 1967

Stand 7 is situated at the base of a gentle slope bordering a drainage channel which connects Buck and Honeymoon Lakes. The stand is itself on relatively flat land. Upslope it is bounded by a moist lodgepole pine-spruce forest. On the opposite side is muskeg peatland which occupies most of the drainage channel. The stand is located in an ecotone separating the two types of vegetation.

Stand 8 Jasper 117°39'; 52°33' Alt.= 1387 m (4550 ft)
 July 27 - 28, 1967

This stand is located 0.5 km NE of Sunwapta Falls, alongside the Jasper-Banff highway. It occupies a muskeg-filled drainage channel linking Buck Lake with the Sunwapta River. The channel varies between 50 and 100 m in width. A small sluggish stream runs alongside the stand. North of the stand is a sedge mat extending out into Buck Lake (see Plate III, Photo 2). The channel is bordered on one side by the highway embankment; on the other by a gentle slope bearing lodgepole pine, black spruce and white spruce.

Stands 9, 16 Banff 116°53'; 52°03' Alt.= 1448 m (4750ft)
 July 31 - Aug. 3, 1967; July 27 - 28, 1968

These two stands, though located in "lowland", share the greatest elevation of the 16. They are situated approximately 15 km NW of the Saskatchewan River Crossing



PLATE III

Photo 1. Streambed and shallow wooded peatland in vicinity of Stands 5 and 6, base of Athabasca River valley, Jasper Park.

Note presence of lodgepole pine in background.

Photo 2. Wet *Carex* community and adjacent lodgepole pine - black spruce forest near south end of Buck Lake, Jasper Park.

A gentle upland slope rises towards the right. The dominant sedge in the foreground is *Carex rostrata*. Stand 8 abuts this sedge community.

in northern Banff Park and 200 m S of the Rampart Creek campground, alongside the Jasper-Banff highway. They occupy flat alluvial deposits laid down by the North Saskatchewan River and are separated by a distance of between 5 and 25 m. To the west (towards the river) they are bordered by a broad, treeless band of more recently deposited alluvial material, through which many small streams pass on their way to the river.

Stand 10 Jasper 118°05'; 53°12' Alt.= 1265 m (4150 ft)
Aug. 16 - 18, 1967

Stand 10 is located approximately 1 km NNW of Princess Lake, alongside an access road paralleling the Snake Indian River. The stand occupies the base of a small depression (about 100 m wide) surrounded by gently sloping uplands which are occupied by moist pine-spruce forest. There are no streams entering or leaving the depression, which is occupied by a muskeg type of vegetation.

Stand 11 Jasper 118°17'; 53°19' Alt.= 1342 m (4400 ft)
Aug. 19 - 21, 1967

Stand 11 is located about 1 km east of the Snake Indian Falls, on a very (5°) gentle upland slope. On one side it is bordered by a narrow stream (1 m wide) and on the other by a moist sedge meadow which overlies a shallow peat deposit. Surrounding uplands are covered with moist lodgepole pine - white spruce forest.

Stands 12, 13 Jasper 118°19'; 53°21' Alt.= 1341 m (4500 ft)

Aug. 21 - 28, 1967

These two stands are located alongside the Snake Indian River, about 4 km south of the confluence of Willow Creek and the river. Though the 2 stands are immediately adjacent, they are quite different. While Stand 12 is situated in muskeg, Stand 13 occupies a gentle upland slope (10°) bordering the peatland.

Stand 14 Jasper 118°13'; 53°15' Alt.= 1234 m (4050 ft)

Aug. 29 - 30, 1967

This stand occupies a small muskeg-filled depression (50 x 200 m) located alongside the Snake Indian Road about 1 km north of the Shale Banks warden cabin. There are no streams in the vicinity and the depression is completely surrounded by upland pine-spruce forest.

Stand 15 Jasper 117°54'; 52°39' Alt.= 1320 m (4330 ft)

July 22 - 23, 1968

This stand is situated on the east-facing slope of the Athabasca River valley, about 4 km above the base of the Geraldine Lake road. The stand occupies a level portion of this slope. On one side it is bordered by one of a chain of small muskegs while on the other it is bordered by a gentle slope (5°) occupied by pine and spruce.



PLATE IV.

Photo 1. Interior of Stand 16.

The dominant trees are black spruce, lodgepole pine and white spruce in this dark feathermoss forest.

Photo 2. A mesic upland lodgepole pine - black spruce forest in the lower subalpine zone, vicinity of Athabasca Falls, Jasper Park.

The dominant shrub is *Shepherdia canadensis*.

VII. Ordination and Tentative Classification of Stands

A. Introduction

The vegetational relationships between the biotic communities of an area can be assessed by a wide variety of techniques. At one end of the available spectrum are the more or less discrete techniques which operate on the practical assumption that vegetation is essentially discontinuous in nature. This hypothesis may be theoretically valid in instances in which controlling environmental factors are discontinuously distributed, as well as practically valid when the vegetation of a large area is being described.

However, as the scope of the study is narrowed and the intensity of observation increased, it is often found that the vegetation is in fact partially continuous in character, exhibiting gradual changes along environmental gradients as well as sharp breaks at environmental discontinuities. In extreme cases of continuous variability the delineation of "community types" tends to become increasingly arbitrary and prone to personal experience and philosophical bias.

In most fairly intensive studies it is probably best to assume at least some continuity in vegetation and to use a technique which will expose and express this continuity, if indeed it is present. The results of these techniques often suggest that a discrete classification is, in the final instance, the best vehicle for summarizing the information.

The technique known as "simple ordination" (*sensu* Orloci 1966) is one of the crudest of these techniques. Nevertheless

it has been employed with considerable success in many studies of vegetation. Beil (1966) and Stringer (1966), working in forest communities of Jasper and Banff Parks, both found that a simple ordination of stands was a satisfactory medium for expressing vegetational variation in relation to selected environmental factors. Hnatiuk (1969), however, had little success with simple ordination in his analysis of Jasper and Banff lodgepole pine communities and found a more sophisticated technique known as "factor analysis" to be much more satisfactory, when used in combination with a classification system.

Following the field work, I felt that a crude classification system could be applied with success to my black spruce communities. I decided to test this assumption by means of a stand ordination.

B. Construction of Stand Ordination

The technique I used was essentially that of Bray and Curtis (1957) with modifications in construction as described in Orloci (1966). In this technique stands are positioned relative to each other in space according to their overall vegetational similarity. The degree of similarity between any two stands is expressed as a single numerical value. The most commonly used expression is the "Index of Similarity":

$$I = \frac{200w}{a+b}$$

where "w" represents what the two stands have in common (i.e., shared attributes) and "a" and "b" represent the separate sums of attributes of the two stands. The maximum theoretical similarity value is 100, which would arise if a stand was compared to itself at the same point in time with

no sampling error.

The first step in ordination is one of subjectively deciding what kind of and how much information will be used in calculating the similarity values. This is probably the most significant step, as the nature of the results can only be interpreted relative to initial information input.

I chose to base the similarity values on the quantitative performance, as indicated by cover and frequency, of the shrub and herb species. Information on bryophyte and tree species was omitted for two reasons. First, I was interested in studying the performance of these species on an ordination which did not include them in its composition. Secondly, no frequency data were available for bryophytes, and frequency data of tree species was measured on a much different scale than that for herbs and shrubs. If the bryophytes and trees had been included, this would have necessitated "relativizing" the different strata, which I felt could result in difficulties of interpretation.

Each shrub and herb species population within each stand was given a "Prominence Value" according to the following equation:

$$P = [\% \text{ Cover} \times (\% \text{ Frequency})^{\frac{1}{2}}] + 1$$

This synthetic expression of species performance was introduced by Beals (1960) and modified by LaRoi (1964) for studies of plant communities. The Prominence Value stresses cover as a prime attribute in the assessment of population size in the vegetation complex. Frequency plays a modifying

role, as an index of dispersion, and also compensates some species which, due to their erect growth form, may have high density and/or standing crop and yet low cover (e.g., *Juncus balticus*).

A matrix of similarity values was computed using a Fortran IV program designed by Ream (1962) which is on file in the Plant Ecology Laboratory, Department of Botany, University of Alberta.

The next step was to convert the matrix of similarity values into a geometrical model. First, the similarity values were transformed into a measure of distance, so that stands are separated by a distance inversely proportional to their degree of similarity. The technique used was to convert each "Index of Similarity" to an "Index of Dissimilarity" as follows:

$$\text{Index of Dissimilarity} = 100 - I$$

The matrix of dissimilarity values is presented in Appendix A.

There are a number of closely related geometrical techniques of constructing a simple ordination. I chose the one developed by Orloci (1966), as it results in a truly right-angle X - Y coordinate system. This is of value in accurately calculating interstand distances within the ordination.

The steps involved in constructing the 2-dimensional stand ordination from the matrix of dissimilarities are presented in Appendix B, as are the resulting X- and Y-

coordinates of the 16 stands. The ordination is presented in Figure 4.

The test of the geometrical adequacy of any ordination lies in its accuracy in portraying the matrix of dissimilarity values (Newsome and Dix 1968). A correlation coefficient was calculated between interstand distances in the ordination and corresponding dissimilarity values. Fifty stand pairs were randomly chosen and the r -value obtained was +0.84, significant at the 99% level of confidence. The ordination is thus a very satisfactory pictorial representation of the matrix of dissimilarities.

It is well to point out here some of the qualifications in interpreting an ordination.

Bray and Curtis (1957) state:

"When coefficients of community are used....as indicators of spatial distance, then exact interstand distances are not available, since the position of a stand in relation to another stand occurs within an area of uncertainty originating in the sampling error made in surveying the stands."

Another problem is more geometrical in nature. The Index of Dissimilarity ($100 - \frac{200w}{a+b}$) is not a true measure of Euclidean distance. Due to this fact, problems have occurred in the construction of some ordinations. However, such problems were not encountered in the construction of the ordination presented in this thesis. Also, Newsome and Dix (1968) point out that the Index of Dissimilarity is to be preferred to an Euclidean formula developed by Austin and Orloci (1966) which is geometrically more sound but which

appears to be less meaningful ecologically.

C. Tentative Classification

Some of the more significant vegetational, physiognomic, and edaphic features of the stands are discussed below in relation to the proposed classification. This information is provided solely for the purpose of orienting the reader to the classification and its relation to the ordination. More detailed data are presented in following sections of the thesis.

Extending from the top to the centre of the ordination is a cluster of stands (Nos. 5, 14, 8, 10, 9, 12) which are closely similar in vegetation, soil moisture status, and physiognomy. These stands exhibit:

- 1) A pronounced hummock-hollow type of microtopography. The hummocks are composed of organic matter, predominantly moss peat.
- 2) A relatively wet soil moisture regime at the surfaces of the hollows, grading to "moist" at the hummock tops.
- 3) A noticeably "clumped" dispersion of trees. Tree height averages between 3 and 10 m. The tree stratum is clearly dominated by black spruce.
- 4) A well-defined medium shrub stratum dominated by *Ledum groenlandicum* and/or several species of *Salix*.
- 5) A well-developed, floristically rich herb-dwarf shrub stratum dominated by species of *Carex*, the most prominent of which are *C. vaginata*, *C. gynocrates* and *C. aquatilis*.

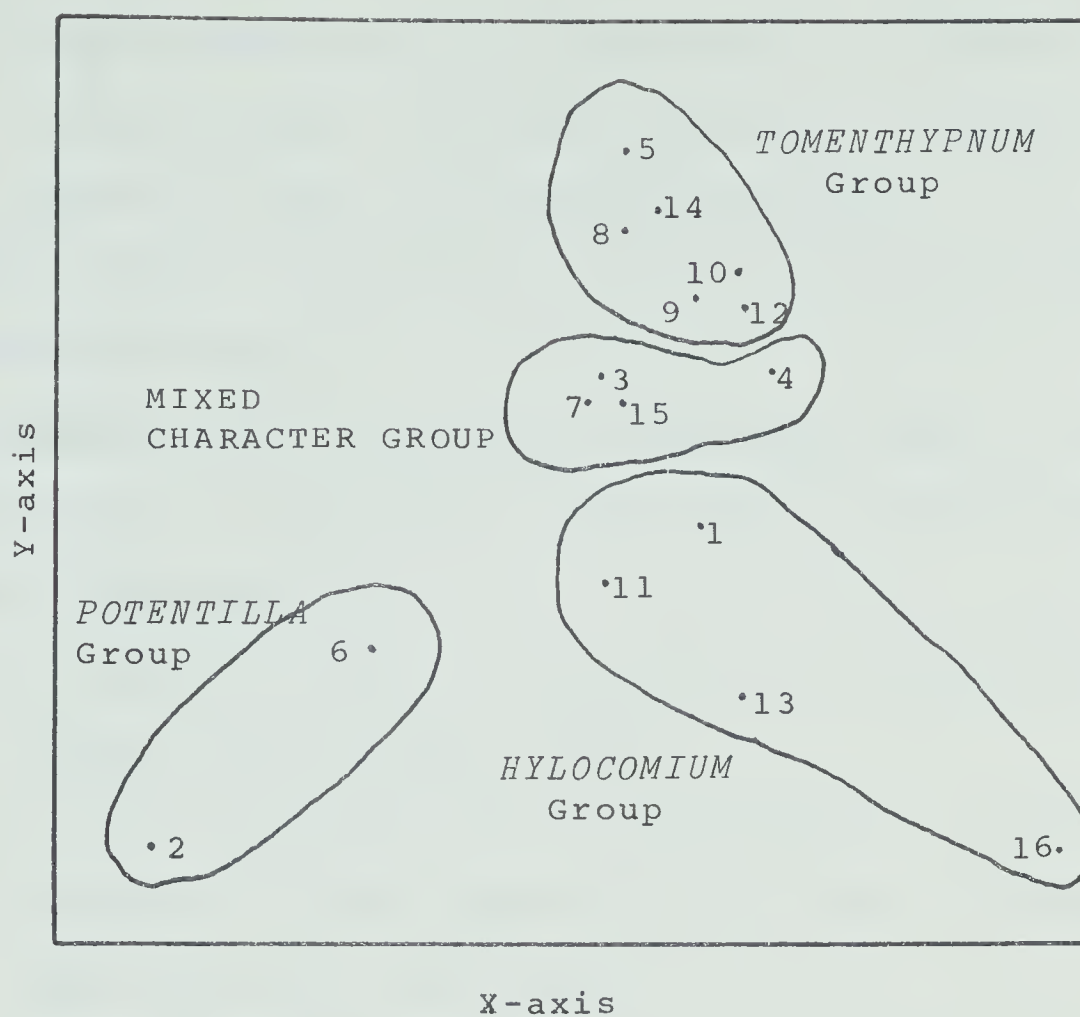


FIGURE 4. The Ordination, showing location of Stands and Groups.

- 6) A well-developed moss stratum which is dominated by wetland mosses. The most important of these, in terms of cover, is *Tomenthypnum nitens*.

This cluster of 6 stands will be referred to as the "TOMENTHYPNUM" Group.

Extending from the centre to the lower right of the ordination are 4 stands (Nos. 1, 11, 13, 16) which share the following characteristics:

- 1) A "mesic" to moist (relative to the *TOMENTHYPNUM* Group) soil moisture regime.
- 2) A lack of pronounced microtopography. The ground surface is gently undulating to level. Mineral soil lies near the surface.
- 3) A true arboreal "canopy" of tree foliage (in contrast to the stands in the *TOMENTHYPNUM* Group). The stands have a diffuse, medium-to-low intensity light regime throughout (Stand 16 is the darkest of all stands). White spruce and lodgepole pine are important components of the tree stratum. All tree species exhibit a degree of natural pruning of the lower branches. The trees average over 8 m in height.
- 4) Poorly developed medium shrub and herb-dwarf shrub strata.
- 5) A medium to well-developed moss stratum dominated by feathermosses, predominantly *Hylocomium splendens* and *Pleurozium schreberi*. (Stand 11 is an exception here, having a poorly developed moss carpet).

This cluster I have termed the "*HYLOCOMIUM*" Group.

A third cluster of stands (Nos. 3, 4, 15, 7) occupies the centre of the ordination and separates the "*TOMENTHYPNUM*" and "*HYLOCOMIUM*" Groups. Their central position in the ordination suggests that these stands are intermediate in character between the *TOMENTHYPNUM* and *HYLOCOMIUM* Groups.

Stand 3 has a hummocky microtopography and a clumped dispersion of trees. The hummocks have a mineral core which is capped by organic matter and appear to have first developed through frost heaving. The hummocks are relatively steep-sided and the hollows flat-bottomed, in contrast to the more rolling hummock-hollow microtopography typical of the *TOMENTHYPNUM* Group. The hollows are damp to wet throughout the summer, whereas the tops of hummocks are much drier. This stand is much more similar to stands of the *TOMENTHYPNUM* Group than those of the *HYLOCOMIUM* Group. However, the peculiar type of microtopography and combined mineral-organic nature of the hummocks have had enough effect on the vegetation that the stand cannot be included in the *TOMENTHYPNUM* Group. If it were, the relative homogeneity of the group would be destroyed.

The "intermediate" character of Stand 4, reflected in its central position within the ordination, arises from the fact that one end of the stand has the characteristics of the *HYLOCOMIUM* Group while the other end is similar to Stand 3. The centre of the stand features a subtle interdigitation of the two types of vegetation and physiography.

Stand 7 is located in a "tension zone" between a

TOMENTHYPNUM-type muskeg community on one side and an upland *HYLOCOMIUM*-type forest on the other. The stand is composed of a mosaic of the two communities.

Stand 15, like Stand 7, is composed of a complex mosaic of two different communities. Some portions of the stand bear a closed-canopy tree stratum with low shrub and herb cover but a well-developed moss stratum. The other component of the mosaic is an open muskeg-like community, with clumped trees, a well-developed medium shrub stratum dominated by *Ledum groenlandicum* and a more hummocky microtopography. The dominant moss in both units of the mosaic is *Hylocomium splendens*.

The above 4 stands comprise the "Mixed Character" Group. It is a highly heterogeneous composite and thus lacks a positive identity of its own. It contains the 3 least homogeneous stands of the 16 (Nos. 4, 15 and 7). The stands have little in common except that they occupy the centre of the ordination and do not wholly belong in either the *TOMENTHYPNUM* or *HYLOCOMIUM* Groups. The main benefit obtained from creating this group is that the homogeneity of the other groups is maximized as a result.

Stands 6 and 2, located in the lower left of the ordination, are much more similar to each other than they are to any of the other stands. They share the following characteristics:

- 1) A well-developed hummock-hollow type of microtopography. The hummocks are composed almost entirely of heavy mineral soil and have developed through

frost heaving.

- 2) A dry to almost xeric soil moisture regime on the tops and sides of the hummocks, the hollows being dry to slightly moist.
- 3) A poorly developed tree stratum. These stands have a much lower tree density than the other 14. The trees exhibit a clumped dispersion.
- 4) A very conspicuous medium shrub stratum dominated by *Potentilla fruticosa*.

Stands 6 and 2 differ in their moss carpets. Stand 6 has a patchy, turfy moss layer dominated by *Ditrichum flexicaule* and *Campylium stellatum*. Stand 2 lacks a moss carpet, although small scattered patches of turf moss are present.

These two stands comprise the "POTENTILLA" Group.

D. Vegetational-Environmental Continua

The above discussion emphasizes the presence of discontinuities in black spruce-dominated vegetation. I have used these discontinuities to delimit three well-defined groups of stands and another mixed character aggregate. I believe this treatment is in accord with impressions gained during the Preliminary Reconnaissance and subsequent field work. It was noted that in the lowlands of the two parks, the vegetation changed very rapidly with slight changes in relief and soil conditions. The rapidity of this change is well exemplified by Stands 5 and 6, which are in very close proximity but are very different in physiognomy, vegetation

and soils. Rarely were gradual, orderly transitions between vegetation types seen in the field. Muskeg communities, such as the stands of the *TOMENTHYPNUM* Group are, in general, clearly recognizable. Also recognizable and distinct are the upland feathermoss forests. Usually, however, these two community-types do not merge in a continuous manner. Rather the nature of the transition is more that of a mosaic or interdigitation of the two types.

Thus the stands of the "Mixed Character" Group do not in general represent a central portion of a vegetational-environmental continuum but rather community mosaics with a differentproportional representation of relatively integrated communities.

It is significant that although the ordination was constructed solely from performance data for shrub and herb species, the distribution of stands is a very natural one in terms of physiognomy, soils and nature of moss stratum. This implies a high degree of correlation between the nature of the shrub and herb strata and the overall vegetational and edaphic characteristics of the ecosystem.

E. Tabular Arrangement of Stands

In order to facilitate translation between tabular data and positions of stands within the ordination, I have arranged the stands in each Group in decreasing order, according to their Y-axis coordinates in the ordination. An exception to this arrangement will be presented in the discussion of the tree stratum.

VIII. SOILS

The information on edaphic environmental components is drawn from four sources:

- 1) Visual estimates (e.g., estimated microrelief, gravel volume)
- 2) Soil pits - one per stand
- 3) Surface Core Samples - twenty per stand
- 4) Water samples

A. Microtopography, Depth to Water Table and Mineral Soil

TOMENTHYPNUM Group (Stands 5, 14, 8, 10, 9, 12) - these 6 stands are characterized by a hummock-hollow type of microtopography in which the hummocks are composed primarily of moss peat. The estimated microrelief (i.e., vertical distance between hummock-top and base of hollow) ranges between 30 and 50 cm. Depth to water table from hummock-top averaged about 50 cm in the summer of 1967. While Stand 5 contained large amounts of standing water in both 1967 and 1968, standing water was uncommon in the other 5 stands during both summers. Information from soil pits dug in hollows indicates that mineral soil lies within 30 cm of the surfaces of the hollows in all stands but No. 14, in which depth of peat exceeded 2 m. The water table was above the mineral layers in all stands of the Group. As a result, horizons exhibited the blue-grey colour associated with water-saturated mineral soil.

HYLOCOMIUM Group (Stands 1, 11, 13, 16) - the surface

TABLE 1.

FOOTNOTES:

Code: - "HUMM-HOLL - hummocky microtopography;

"UND" = undulating - more gradual transition from
high to low points than HUMM-HOLL type;

"LEV" = level - microtopography not pronounced.

* - based on spot measurements in field - represents
average vertical distance between high and low
points (e.g. hummock-top to hollow base).

** - depth to water table measured from hummock-tops
in hummocky stands.

TABLE 1. Microtopographic Features; Depths to Water Table

Group	Stand	Type of Microtopo- graphy	Composition of Hummocks	Average* Micro- relief (cm)	Depth to Water Table**
<i>TOMENTHYPNUM</i>					
	5	HUMM-HOLL	Organic	50	July 8/67 - 25 cm
	14	HUMM-HOLL	Organic	50	Aug. 29/67 - 75 cm
	8	HUMM-HOLL	Organic	30	July 27/67 - 38 cm; Sept. 4/67 - 55 cm
	10	HUMM-HOLL	Organic	50	Aug. 16/67 - 90 cm
	9	HUMM-HOLL	Organic	30	July 31/67 - 45 cm
	12	HUMM-HOLL	Organic	30	Aug. 24/67 - 45 cm
<i>MIXED CHARACTER</i>					
	3	HUMM-HOLL	Organic+mineral	50	July 3/67 - 75 cm; July 17/68 - 50 cm
	4	HUMM-HOLL;UND	Organic+mineral	30	July 4/67 - 55 cm
	15	HUMM-HOLL;UND	Organic	45	July 22/68 - 75 cm
	7	UND-LEV	---	25	July 27/67 - 38 cm
<i>HYLOCOMIUM</i>					
	1	UND	---	25	June 14/67 - 30 cm
	11	LEV	---	10	Aug. 19/67 - 102 cm+
	13	LEV	---	10	Aug. 26/67 - 60 cm+
	16	UND	---	25	July 27/68 - 50 cm
<i>POTENTILLA</i>					
	6	HUMM-HOLL	mineral	50	July 16/67 - 125 cm; July 26/68 - 65 cm
	2	HUMM-HOLL	mineral	35	June 26/67 - 90 cm+; July 17/68 - 85 cm

of the moss or mineral soil is gently undulating to level. The water tables stood at a depth of 30 cm and 50 cm in Stands 1 and 16 respectively (see Table 1), while in Stands 11 and 13 it was deeper than 102 cm and 60 cm. Soil pit and surface core data indicate that mineral soil lies within 15 cm of the surface in all 4 stands. The mineral horizons above the water tables of Stands 1 and 16 exhibit spotty ferric iron stains; the water table must occasionally rise above the topmost mineral horizons in these stands. The upper mineral horizons of Stands 11 and 13 exhibit no such gleization and can be termed "upland" in site characteristics.

MIXED CHARACTER Group (Stands 3, 4, 15, 7) - as these stands are the least homogeneous of the 16, it is difficult to generalize about them. Their individual microtopographies have already been adequately described (see p. 47). Depth to water table ranges between 38 cm and 75 cm (see Table 1). The depth of organic matter is also a highly variable quantity in these stands. Soil pit data, which is not too reliable owing to the mosaic nature of the stands, indicate that the maximum depth to mineral horizons was 38 cm, in Stands 3 and 4. However, during surface core sampling it was noted that mineral soil lies within a few cm of the surface in portions of all 4 stands.

POTENTILLA Group (Stands 6, 2) - these stands, like those of the *TOMENTHYPNUM* Group, exhibit a conspicuous hummock-hollow microtopography. The hummocks are composed of mineral soil, however, and have probably developed

through frost-heaving. Hummock-hollow microrelief is of approximately the same magnitude as that of the *TOMENTHYPNUM* stands. Depth to water table from hummock-top in 1967 was 125 cm in Stand 6 and greater than 90 cm in Stand 2. The 1968 levels are probably more typical - depths of 65 cm and 85 cm in Stands 6 and 2 respectively. Weak glei mottling is present between a depth of 10 cm and the water table in both stands, indicating that the water table has occasionally approached the bases of the hollows.

B. Texture of Mineral Horizons; Gravel Fraction

Data from soil pits (presented in Table 2) indicates a high proportion of sand and silt in the 2 mm fraction of the mineral horizons of all stands. Most of the mineral horizons fall in the silt loam, sandy loam and loam textural classes. Clay content is in all cases less than 25%, with the exception of horizon C of Stand 11. The average clay content of the top mineral layers of all stands is 11%, while silt and sand content each average 45%.

TOMENTHYPNUM Group (Stands 5, 14, 8, 10, 9, 12) - the mineral horizons of the 6 stands are composed almost entirely of particles less than 2 mm in size. Visual estimates indicate that Stand 10 is the only one in which gravel (particles larger than 2 mm; the term is used here in a very broad manner) volume reaches 10%. Volumetric gravel fractions in the other 5 stands are all less than 1%. The low gravel content of the *TOMENTHYPNUM* stands is due to the fact that most of the mineral horizons have been

C. Soil and Water Chemistry

Water sample data, presented in Table 4, indicates that the soil water from all stands shares the following chemical features:

1) High concentrations of the cations calcium and magnesium in the form of dissolved bicarbonates and carbonates. This is evident from data on "calcium hardness", "magnesium hardness" and "total hardness", all of which are expressed in ppm. CaCO_3 . "Calcium hardness" may be converted to ppm calcium by multiplying the tabulated figures by 0.4.

Total hardness (1968) ranges from 107 ppm in Stand 15 to 376 ppm in Stand 3 and averages 218 ppm over the 14 stands from which samples were obtained.

2) Slight alkalinity. The pH in 1968 ranges from 7.2 to 8.1 and 1967 values are similar. The alkalinity is predominantly due to the carbonates and bicarbonates of calcium and magnesium. The difference between "Alkalinity" and "Total Hardness" is a measure of the concentration of sodium salts. This difference is slight in all samples.

Data from soil pits and surface core samples (Tables 2 and 3) indicate that the solid component of the soil contains large cation concentrations. Unfortunately, there is no quantitative data on "free" calcium and magnesium. Qualitative tests with dilute HCl do suggest that "free lime" is relatively abundant but highly variable with depth. Soil pH data also suggests large amounts of cations, mainly

TABLE 2. Textural and Chemical Properties of Soil Pit Horizons

Stand	Horizon	Depth of Horizon	Texture			Class	Nutrients in kg/ha (except for Free Lime)				Conduc- tivity in mmhos/cm	pH
			% Sand	% Silt	% Clay		Avail	Avail	Free	Ca		
							N	P	K			
TOMENTHYPNUM GROUP												
5	A	0-10	--	--	--	organic	6	6	381	9	0.6	7.0
	B	10-61	52	26	22	loam	0	0	96	2	0.3	7.9
14	A	0-15	--	--	--	organic	0	2	123	0	0.3	7.2
	B	15-30	--	--	--	organic	0	2	62	0	0.5	7.3
	C	30-200	--	--	--	organic	0	2	45	0	0.5	6.7
8	A	0-28	--	--	--	organic	25	13	66	0	0.5	7.0
	B	28-33	42	50	8	silt loam	3	2	13	1	0.3	7.4
	C	33-46	74	16	10	sandy loam	1	2	83	0	0.3	7.1
	D	46-55	30	64	6	silt loam	0	1	22	0	0.2	7.7
	E	55-60	74	14	12	sandy loam	0	6	36	0	0.2	7.6
10	A	0-20	--	--	--	organic	2	6	66	0	0.5	7.2
	B	20-48	--	--	--	organic	2	6	31	0	0.4	7.0
	C	48-66	26	66	8	silt loam	2	8	18	0	0.2	7.5
	D	66-91	26	66	8	silt loam	1	2	78	6	0.3	8.3
9	A	0-30	--	--	--	organic	8	2	149	8	0.5	7.3
	B	30-61	46	44	10	sandy loam	--	--	--	-	--	--
12	A	0-30	--	--	--	organic	2	6	87	0	0.5	7.1
	B	30-44	46	44	10	sandy loam	1	2	92	0	0.3	7.6
	C	44-114	--	--	--	organic	2	2	49	0	0.3	7.4
MIXED CHARACTER GROUP												
3	A	0-8	--	--	--	organic	8	21	363	0	1.5	6.0
	B	8-38	--	--	--	organic	6	8	18	0	0.9	6.9
	C	38-69	46	40	14	loam	1	8	58	5	0.7	7.7
	D	69-97	54	28	18	sandy loam	2	6	110	5	0.5	8.0

TABLE 2. cont'd.

Stand	Depth of Horizon (cm)	Texture			Nutrients in kg/ha (except for Free Lime)						Conductivity in (mmhos/cm)	pH
		Sand %	Silt %	Clay %	Class							
					Avail N	Avail P	Avail K	Free Ca	Free			
4	A	--	--	--	1	2	22	0	0.5	7.4		
	B	34	56	10	0	2	66	1	0.5	7.6		
	C	64	22	14	0	2	58	6	0.4	7.8		
15	A	--	--	--	1	12	158	0	0.4	6.1		
	B	--	--	--	9	6	101	0	0.3	6.7		
	C	50	42	8	3	1	62	0	0.2	6.9		
7	A	--	--	--	16	6	276	0	0.6	7.5		
	B	44	50	6	7	2	83	0	0.2	7.9		
	C	56	30	14	0	1	49	6	0.3	8.0		
HYLOCOMIUM GROUP												
1	A	--	--	--	6	11	180	0	0.4	5.6		
	B	66	22	12	0	6	66	0	0.1	7.3		
	C	66	22	12	0	2	92	1	0.2	7.6		
11	A	--	--	--	1	2	87	6	0.5	7.8		
	B	36	48	16	1	2	87	7	0.3	8.1		
	C	12	20	68	0	1	220	8	0.4	8.0		
13	A	46	46	8	1	19	69	0	0.2	5.7		
	B	64	14	22	0	21	175	0	0.2	6.8		
	C	76	14	10	0	8	92	3	0.3	7.3		
16	A	--	--	--	0	18	35	0	0.4	4.5		
	B	30	60	10	0	1	83	6	0.3	7.7		
	C	52	38	10	0	1	49	7	0.2	8.1		
POTENTILLA GROUP												
6	A	60	32	8	4	2	149	3	0.3	8.0		
	B	50	34	16	0	2	62	1	0.3	8.4		

TABLE 2. cont'd.

Stand	Depth of Horizon (cm)	Texture			Class	Nutrients in kg/ha (except for Free Lime)					Conduc- tivity in pH
		Sand %	Silt %	Clay %		Avail					
						N	P	K	Free CA	(mmhos/cm)	
6 C	89-104	96	2	2	sand	0	2	22	2	0.2	8.6
D	104-109	34	48	18	loam	0	2	49	1	0.3	8.5
2 A	0-8	48	42	10	sandy loam	9	2	87	7	0.5	7.8
B	8-33	50	34	16	loam	1	2	101	7	0.5	8.1
C	33-36	--	--	--	--	0	2	119	7	0.6	8.1
D	36-51	80	12	8	loamy sand	1	2	58	8	0.5	8.0
<hr/>											
Surface Horizon	MEAN	--	--	--	--	5.6	8.1	143.6	-	0.51	
(all Stands)	S.D.	--	--	--	--	6.8	6.7	108.9	-	0.28	
<hr/>											
Top Organic											
Horizon (of 13											
Stands)	MEAN	--	--	--	--	6.5	7.8	148.9	-	0.55	
	S.D.	--	--	--	--	7.2	6.2	119.1	-	0.30	
<hr/>											
Top Mineral											
Horizon (of											
above Stands)	MEAN	43.2	45.7	11.2		1.6	3.1	65.8	-	0.31	
	S.D.	10.8	12.7	4.4		2.1	2.8	27.9	-	0.16	
<hr/>											
Top Mineral											
Horizon (all											
Stands)	MEAN	44.8	44.5	10.9		2.3	4.1	73.5		0.31	
	S.D.	10.5	11.8	4.1		2.8	5.0	33.2		0.15	

TABLE 3. Textural and Chemical Properties of Surface Core Samples (0-15 cm)

Stand	Texture			Class	Nutrients in kg/ha (except for Free Ca)							Conduct (mmhos)	pH	Sampling Date
	%	Sand	Silt		Clay	N	P	K	Total	Free				
											Ca*			
TOMENTHYPNUM GROUP														
5	44	40	16	loam	0	13	158	414	1	2.5	6.7	July 26/68		
14	--	--	--	organic	1	56	149	437	0	2.6	6.6	July 19/68		
8	--	--	--	organic	1	28	83	358	0	3.1	6.0	July 25/68		
10	--	--	--	organic	1	62	119	392	0	2.1	6.3	July 19/68		
9	52	38	10	sandy loam	0	18	119	414	2	2.6	6.2	July 25/68		
12	--	--	--	organic	3	58	193	426	-	2.6	6.4	July 18/68		
MIXED CHARACTER GROUP														
3	58	34	8	sandy loam	7	36	180	448	3	3.1	6.5	July 17/68		
4	58	34	8	sandy loam	1	28	180	426	0	1.8	6.7	July 17/68		
15	--	--	--	organic	1	44	137	370	0	1.6	5.9	July 22/68		
7	50	42	8	sandy loam	0	13	128	336	0	2.5	6.4	July 25/68		
HYLOCOMIUM GROUP														
1	58	34	8	sandy loam	1	30	162	336	0	2.8	6.2	July 26/68		
11	54	34	12	sandy loam	1	56	132	403	1	3.4	6.6	July 19/68		
13	48	40	12	loam	0	68	141	336	0	1.8	5.5	July 18/68		
16	44	46	10	sandy loam	0	16	114	392	4	1.8	6.6	July 27/68		
POTENTILLA GROUP														
6	48	30	22	loam	0	2	158	403	5	1.6	7.2	July 26/68		
2	56	32	12	sandy loam	1	6	175	414	4	3.2	7.1	July 17/68		
MEAN														
						32.1	146	394						
60.														

- = no analysis because of high organic matter content.

* - "Free Lime" was evaluated on the basis of reaction to HCl. A nine point scale was used;
1 = trace and 9 - very high.

TABLE 4. Chemical Characteristics of Soil Water

Group	Stand	Total Hardness 1967	Ca Hardness 1967	Mg Hardness 1967	Alkal- inity 1968	pH 1967	1968	Nitrate 1967	1968	Phos- phate 1967	Iron 1968
<i>TOMENTHYPNUM</i>											
	5	320	220	245	75	221	7.6	7.4	0	0.2	0.16
	14	260	238	210	50	250	7.7	7.6	0	0.3	0.27
	8	165	140	125	40	143	6.8	7.5	0	0.6	0.12
	10	---	285	---	--	287	---	6.6	-	---	0.18
	9	235	253	205	30	227	7.4	7.6	0	0.2	0.10
	12	295	238	200	95	251	7.6	7.5	0	0.2	0.10
<i>MIXED CHARACTER</i>											
	3	455	376	365	90	296	8.3	7.6	10.2	2.7	0.5
	4	305	279	240	65	246	7.7	7.6	0	0.3	0.10
	15	---	107	---	--	115	---	7.2	-	---	0.12
	7	180	113	130	50	127	7.5	7.4	0	0.4	0.07
<i>HYLOCOMIUM</i>											
	1	90	130	80	10	121	7.9	7.5	0	0.2	0.18
	11	290	222	195	95	220	8.3	8.1	0	0.2	0.10
	13	---	---	---	--	---	---	---	-	---	---
	16	---	221	---	--	215	---	7.4	-	---	3.65
<i>POTENTILLA</i>											
	6	255	---	185	70	---	7.8	---	0	0.3	---
	2	195	227	160	35	165	7.9	7.6	0	0.1	0.10

- "Total", "ca", and "Mg" Hardness and "alkalinity" are all expressed as ppm CaCO₃.
Nitrate, Phosphate and Iron are expressed in ppm.

- a blank space indicates that a sample was not obtained.

in the form of carbonates. The great majority of pH values from soil pit horizons fall in the 6 to 8 range. The lowest found was 4.6, in horizon A of Stand 16, while the highest was 8.6 in horizon C of Stand 6.

The pH of the surface horizon is less than that of any subsurface layer in 13 of the 16 stands; in all soil profiles with both mineral and organic horizons the latter always have lower pH's, as would be expected.

The surface core samples in general have a lower pH than the superficial soil pit layers. Possibly this is due to the fact that most soil pits were dug in 1967 while core samples were all taken in 1968. The summer of 1967 was hot and dry, favouring the accumulation of salts near the soil surface. Precipitation was much greater in 1968 - conditions would be more favourable for leaching, resulting in somewhat lower pH. This explanation cannot be considered complete, however, and the possibility of the differences having arisen from sampling error cannot be ignored.

The concentration of "available potassium" is high in all stands. Average available K of the surface soil pit horizons is 144 kg/ha while surface core samples give an average of 146 kg/ha.

Nitrates are absent from the soil water of all stands but No. 3, which contained 10.2 ppm in 1967 and 2.7 ppm in 1968. I have not arrived at any satisfactory explanation of these high values in this one stand. Moose dung was noted to be more abundant in this stand than in any other

but so many factors can affect the abundance of nitrate that I hesitate to attach real significance to this observation. "Available nitrogen" is highly variable with depth in the soil pits but, with the exception of Stand 15, the greatest concentration is found in the surface horizon. In general, the concentration of available nitrogen is low, averaging 6 kg/ha in the surface horizons of the soil pits. The largest concentration, 25 kg/ha, occurs in horizon A of Stand 8, a member of the *TOMENTHYPNUM* Group.

Any ecological interpretation of soil nitrogen concentration, on the basis of the available data, would be dangerous. Nitrogen compounds are highly labile and soil concentration is affected by a multitude of biotic and physical factors.

"Available phosphorus" seems to be slightly more abundant than available nitrogen. It averages 8 kgm/ha in the surface horizons of the soil pits but, like nitrogen, is highly variable with depth. The largest soil pit concentration is 21 kg/ha, found in horizon A of Stand 3 and horizon B of Stand 13. In contrast to available nitrogen, phosphorus is absent from few soil horizons.

Relatively large difference exist between concentrations of phosphorus in the 1967 surface soil pit horizons and concentrations in 1968 surface core samples. Concentration in the core samples averages 32 kg/ha while that of the surface soil pit horizons averages 8 kgm/ha. All stands but No. 2 have a considerably higher concentration in the

water table lies near the surface of the soil in all of these stands. The upward movement of water and dissolved salts is doubtless facilitated by the "wick-like" nature of the peaty deposits and living moss above the water table. The clumped distribution of trees, their relatively short stature, and the lack of a true canopy of tree foliage suggest that the rate of evapo-transpiration from the ground surface would be high during warm, clear periods (such as the summer of 1967). Consequently a build-up of cations in the surficial layers of peat would be expected during such seasons and pH would tend to be relatively high. During periods of heavy precipitation, this tendency would be reversed.

Based on the above considerations, I hypothesize that pH and concentration of cations in the uppermost soil layers of these stands can be highly variable from year to year and from month to month in any given season. It is doubtful, however, that the surface layers would ever be highly acidic, because of the high cation concentration of the soil water and mineral horizons below the water table. Their edaphic characteristics place the stands in the category of "minerotrophic peatland" (see Section II for a discussion of this type of peatland) and the vegetation type can be termed "muskeg fen", or "wooded fen".

HYLOCOMIUM Group (Stands 1, 11, 13, 16) - these stands, like those of the *TOMENTHYPNUM* Group, have developed on a substrate rich in carbonates. Soil water also contains large

quantities of cations.

The *HYLOCOMIUM* stands differ from the *TOMENTHYPNUM* stands in having a relatively well-developed canopy of tree foliage enclosing a dead air space of considerable depth. Consequently there is much less penetration of direct sunlight to the soil surface and the gradient of relative humidity of air above the ground is probably less steep than in the *TOMENTHYPNUM* stands. As a result, the rate of evapo-transpiration from the ground surface and accumulation of cations in surficial organic layers is probably much less than in the *TOMENTHYPNUM* stands.

The water tables of Stands 1 and 16 lie in close proximity to the surface of the soil and yet the surface organic layer of each stand is highly acidic (pH 5.6 and 4.5 respectively) relative to the surface layers of the *TOMENTHYPNUM* stands. This is explicable on the basis of the greater abundance of needle litter and the lesser importance of cation accumulation in the surface layers of these two *HYLOCOMIUM* stands.

Stand 9 (a *TOMENTHYPNUM* stand) and Stand 16 (a *HYLOCOMIUM* stand) furnish informative contrast. These stands are separated by a distance of only a few meters and are underlain by the same mineral substrate. The water table is near the surface and the soil water is chemically very similar in both stands (see Table 4). Yet the surface layers of organic soil (derived largely from moss) are quite different chemically. Horizon A of Stand 9 has a pH of

7.3, 149 kg/ha of available potassium and a high concentration of free lime, as indicated by reaction to dilute HCl. Stand 16, in sharp contrast, has an A horizon with pH 4.5, only 35 kg/ha potassium and nil free lime. It is important to note that these differences in soil chemistry are largely obscured in the surface core data (see Table 3). This is due to methodology. The cores do not wholly represent the surface "horizon" of soil, which in both stands is organic, but rather the "upper 15 cm" of soil. In both stands many of the cores penetrated and included soil from subsurface mineral horizons. The underlying mineral deposits of both stands are chemically similar and their inclusion in the samples has effectively masked real differences in surface soil chemistry.

The comparison of the surface soil nutrient regime of Stands 9 and 16 suggests that microclimate, as affected by the nature of the tree stratum, may play an important modifying role in regards to the chemistry of the surface soil layers. This would doubtless result in some degree of "feedback" to the vegetation. Although this hypothesis remains to be validated by more intensive research, it appears that overly simplistic cause-effect relationships between vegetation and soil chemistry should not be expected in these wetland communities.

Depth to water table is much greater in Stands 11 and 13. Thus the influence of this water and its dissolved salts on the surface layers of soil should be minimal.

Stand 13 is like Stands 1 and 16 in having a fairly

well-developed carpet of feathermoss and a low pH (5.7) in the surface organic layer. The tree stratum is less well-developed than those of Stands 1 and 16 but better developed than Stand 11. The dead air space enclosed by the tree stratum probably results in a microclimate favouring decomposition of dead moss, with the resultant production of acid, while simultaneously discouraging salt accumulation at the surface. In most parts of the stand the organic matter is slightly moist to the touch. The pH increases rapidly once mineral soil is reached, like Stands 1 and 16.

The tree stratum of Stand 11 is less well-developed than those of the other 3 stands and the surface of the soil is dry enough to favour the establishment of the slow-growing turf mosses rather than feathermoss. Conditions would seem conducive to cation accumulation near the soil surface; the high pH (7.8) in the surface organic layer is therefore not unexpected.

POTENTILLA Group (Stands 6, 2) - both stands exhibit poorly developed tree strata. The water tables are not so deep that their effect on the surface can be ignored. The soil surface is largely mineral. The rate of evaporation from this relatively exposed mineral soil is probably very high during warm, clear weather and this would tend to augment the already high concentration of salts above the water table. Thin white films of salt were occasionally seen on the surface of the hollows of Stand 2 during

1967. This, and the fact that the annual increment of organic matter added to the soil in the form of leaf litter and moss is very low relative to the other Groups undoubtedly accounts in large measure for the high surface pH's of the *POTENTILLA* stands.

D. Surface Soil Moisture Regime in July, 1968.

The information presented in Table 5 and discussed below was obtained from the 20 surface core samples collected from each stand (see Methods). The aim of collecting these data was to enable a comparison, in a relative manner, of the soil moisture regimes of the various stands and Groups. There is no doubt that Total Water Content (TWC) and Excess Water (EW) will vary considerably with time. All data were collected within a short period, however, and I believe that the major differences between soil moisture regimes of the four Groups have been adequately portrayed.

TOMENTHYPNUM Group (Stands 5, 14, 8, 10, 9, 12) - the majority of cores obtained from these stands are composed almost entirely of organic matter, predominantly moss peat. This is shown by the low average oven dry weight (34.2 gms/100 cc core volume). Many of the cores taken from the hollows of Stands 5 and 9 penetrated mineral horizons, however.

TWC (expressed in gms H₂O per 100 cc core volume) is high in all stands, averaging 90.9 gms for the Group. Part of this large quantity can be attributed to sampling error; because of peat compaction under pressure it was difficult in some stands to obtain a high degree of

TABLE 5

FOOTNOTES:

Oven Dry Weight, TWC, BAW, HTW, EW are all expressed as gms per 100 cc core volume.

* V = the "coefficient of variation" =

$$\frac{\text{standard deviation}}{\text{mean}} \times 100$$

Data obtained from Surface Core Camples (0-15 cm).

Samples were collected in July, 1968 (20 per stand).

TABLE 5. Soil Moisture Characteristics (Upper 15 cm)

Group	Stand	O.D. Wt. of Soil			T.W.C			B.A.W.	H.T.W.	E.W.	B.A.W.	H.T.W.	E.W.
		Mean	Std. Dev.	V%	Mean	Std. Dev.	V%						
TOMENTHYPNUM													
	5	33.8	14.0	41.4	98.6	22.2	22.5	17.8	15.4	65.4	18.1	15.6	66.3
	14	20.1	3.1	15.4	97.0	16.4	16.9	6.3	19.0	71.7	6.5	19.6	73.9
	8	24.4	6.1	25.0	96.5	15.9	16.5	11.6	16.5	68.4	12.0	17.1	70.9
	10	20.9	3.5	16.7	82.9	17.0	20.5	9.6	19.6	53.7	11.6	23.6	64.8
	9	80.0	62.9	78.6	85.6	26.1	30.4	17.1	9.3	59.2	20.0	10.9	69.1
	12	26.2	14.2	54.2	84.9	15.5	18.3	9.5	15.9	59.5	11.2	18.7	70.1
Average		34.2		38.6	90.9			12.0	16.0	63.0	13.2	17.6	69.2
MIXED CHARACTER													
	3	35.0	31.3	89.4	62.5	16.5	26.4	13.7	16.6	32.2	21.9	26.6	51.5
	4	27.4	5.1	18.6	68.6	11.4	16.6	13.-	20.8	34.8	19.0	30.3	50.7
	15	27.6	12.5	45.3	83.7	16.4	19.6	9.2	15.0	59.5	11.0	17.9	71.1
	7	47.1	32.9	69.9	65.2	20.1	30.8	42.8	13.5	8.9	65.6	20.7	13.7
Average		34.3		55.0	70.0			19.7	16.5	33.9	29.4	23.9	46.8
HYLOCOMIUM													
	1	39.2	19.8	50.5	59.6	8.1	13.6	10.5	18.9	30.2	17.6	31.7	50.7
	11	46.5	13.8	29.7	51.5	11.6	22.5	13.9	18.6	19.0	27.0	36.1	36.9
	13	71.9	23.1	32.1	21.9	16.4	74.9	12.5	9.3	0.1	57.1	42.5	0.4
	16	90.1	23.8	26.4	48.9	6.9	16.9	19.1	9.2	20.6	39.1	18.1	42.1
Average		61.9		34.7	45.5			14.0	14.0	17.5	35.2	32.1	32.5
POTENTILLA													
	6	98.3	33.2	33.8	46.8	9.7	20.7	25.3	14.5	7.0	54.0	31.0	15.0
	2	70.6	18.2	25.8	32.3	8.6	26.6	17.9	19.2	0	55.4	59.4	0.0
Average		84.5		29.8	39.6			21.6	16.9	3.5	54.7	45.2	7.5

precision. In the wettest stands, standing water covered the surfaces of many hollows. The column of water lying above the soil was included in samples taken from these hollows; it therefore happened that TWC exceeded 100% of core volume in some samples.

The amount of EW is high in all stands. This quantity ranges from 53.7 to 71.7 gms and averages 63.0 gms. Over the 6 stands it accounts for 69.2% of TWC.

BAW and HTW are of approximately the same magnitude and both are much lower than EW. Over the 6 stands BAW averages 12.0 gms and HTW 16.0 gms. They represent 13.2% and 17.6% of TWC respectively. It is apparent that the vegetation of these stands is not likely to suffer a water shortage during anything but the most extended drought. The large amount of EW and consequent poor soil aeration are undoubtedly the most important limiting factor of the edaphic environmental complex.

HYLOCOMIUM Group (Stands 1, 11, 13, 16) - the cores from these stands on the whole contain a high proportion of soil from mineral horizons, as indicated by average oven dry weight (61.9 gms).

TWC is much lower than in the *TOMENTHYPNUM* Group and averages 45.5 gms. The lower value is due to a lesser amount of EW. The BAW and HTW are approximately the same as in the *TOMENTHYPNUM* Group. TWC, EW, BAW, and HTW average 45.5 gms, 17.5 gms, 14.0 gms and 14.0 gms respectively.

Stands 1 and 16, like the *TOMENTHYPNUM* stands, have

abundant water reserves in the forms of a water table close to the surface. The trees may occasionally suffer from poor soil aeration but the possibility of an extended period of water stress is remote.

Stands 11 and 13 probably experience water shortage more often, as the surface layers of soil are remote from the water table and thus more dependent on direct precipitation to maintain moisture above permanent wilting point.

MIXED CHARACTER Group (Stands 3, 4, 15, 7) - in terms of soil moisture characteristics these stands are intermediate between the *HYLOCOMIUM* and *TOMENTHYPNUM* Groups. Oven dry weight averages 34.3 gms but is highly variable within each stand. This is shown by the large average coefficient of variation (V), which, at 55%, is the greatest of the 4 Groups. This is a reflection of the mosaic nature of the soils of these stands. As the water table is near the surface in all 4 stands (though remote from the hummock-tops of Stand 3), the probability of water shortage in summer is low. Abundant EW is present in all stands; poor soil aeration could be limiting to tree growth.

POTENTILLA Group (Stands 6, 2) - the cores from these stands were almost all composed of pure mineral soil. This is reflected in the high oven dry weights - 98.3 and 70.6 gms. Average TWC (39.0 gms) is the least of all Groups. Stand 6 had a slight amount of EW (7.0 gms) while Stand 2 was slightly below Field Capacity at the time of measurement.

Moisture retention characteristics appear to be somewhat better than most *HYLOCOMIUM* and *TOMENTHYPNUM* stands. The surface soil of Stand 6 can, on the average, store 25.3 gms of BAW.

Stands 6 and 2 are probably more drought-prone than any of the others. The very open and sparse nature of the tree stratum would permit rapid evaporation.

IX. THE BRYOPHYTE STRATUM

Species lists of terrestrial mosses, lichens and liverworts are presented in Appendix C. Moss taxonomy follows Bird (1968); that of the liverworts is from Bird (1963) and lichen taxonomy is according to Thomson (1967).

A total of 38 moss species, 3 liverworts and 9 lichens were found in the stands. Liverworts were insignificant in terms of cover and lichen cover never exceeded 5% in any stand and was less than 1% in most. The most abundant lichens were *Peltigera apthosa* and *P. apthosa* var. *leucophlebia*. Due to their relative insignificance, the lichens and liverworts will be omitted from the following discussion.

Cover data for all moss species is presented in Table 6, with species arranged according to % Presence, in decreasing order. The distribution of the cover of *Tomenthypnum nitens* and the distribution of "total feathermoss cover" (3 species) are presented on the stand ordination in Figure 5.

Fourteen of the 38 mosses listed in Table 6 are denoted by asterisks. These species are considered to be calcicolous in habitat preference by Mårtensson (1956), working in Swedish Lapland. It is assumed, there being no evidence to the contrary, that these species have similar habitat preferences on the North American side of the Atlantic.

The abundance of calciphytic mosses, and the fact that some of them (e.g., *Tomenthypnum nitens*, *Sphagnum warnstorffianum*) dominate the bryophyte stratum of a number of stands, tends to substantiate conclusions developed earlier on the

basis of soils chemistry.

The TOMENTHYPNUM Group (Stands 5, 14, 8, 10, 9, 12)

The stratum is very well-developed in all stands. Moss cover ranges between 74% and 97%. The cover-dominant in each stand is the calciphyte *Tomenthypnum nitens*, a fast-growing, hummock-forming species. *T. nitens* appears to resist decay fairly well but there was some evidence of decomposition in hummocks formed by this species. *Tomenthypnum* seems to have a broad moisture tolerance. It is a frequent associate of various species of *Drepanocladus* on floating sedge mats in Jasper and it can also be found on relatively dry upland sites, though rarely. It seems to avoid deep shade, however.

Aulacomnium palustre is closely associated with *T. nitens* in all 6 stands. This species usually forms small tussocks, rarely exceeding a few cm in width, on the moist sides and tops of the *Tomenthypnum* hummocks. Cover of *Aulocomnium* ranges between 5% and 19% in the Group.

Sphagnum warnstorffianum and *S. fuscum* are important components of the moss stratum of 4 of the stands. The maximum combined cover of these is 26% in Stand 12. The two species are closely associated. *S. warnstorffianum* forms the broad base and most of the bulk of the *Sphagnum* hummocks and has a loose, spreading growth habit. *S. fuscum* is largely confined to the tops of the *Sphagnum* hummocks and is much more compact and slow-growing than *S. warnstorffianum*.

The relationship between *S. warnstorffianum* and *T. nitens*

is not clear. In my stands there was no evidence of any successional relationship between the 2 species; they seem to be in a state of competitive equilibrium. In Stands 5 and 12 hummocks of pure *Sphagnum* and pure *Tomenthypnum* grow side-by-side but there was no sign of lateral encroachment by either species. Vertical sections of adjacent hummocks showed that they were composed of one or the other species, but never both. Both species are calciphytes (unlike *S. fuscum*) but *S. warnstorffianum*, by actively secreting acid, can produce acidic hummocks on a calcareous substrate, thus preparing the way for the invasion of acid bog species into what was originally a fen. *Sphagnum fuscum* is no doubt present in the stands because *S. warnstorffianum* has provided a suitably acidic substrate.

It seems likely, from the above consideration, that there would eventually be a succession from *Tomenthypnum* to *S. warnstorffianum* to *S. fuscum* (and other oxylophytic *Sphagna*) with accompanying progression from eutrophy to oligotrophy. Although I could find no direct evidence of this trend in the two parks, it is quite possible that examples of it do occur. Because of the present difficulty of access to many areas in the parks, it will no doubt be many years before the peatland of these areas is completely catalogued, let alone understood. Though this study indicates that much of the peatland is minerotrophic, I am quite convinced, from conversations with park wardens, that some pure *Sphagnum* bogs do exist.

TABLE 6. Percent Moss Cover

GROUPS	MIXED CHARACTER												POTENTIAL					
	TOMENTHYPNUM												HYLOCOMIUM					
STANDS	5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2		
TOTAL MOSS COVER	83	89	97	74	75	84	43	50	80	47	78	59	53	75	51	1		
NUMBER OF SPECIES PRESENT	15	10	7	9	10	10	14	12	7	12	9	8	9	4	7	7		
<i>Tomenthypnum nitenens</i> *	34	73	51	41	23	41	3	9	P	8	P	12	1	P	P			
<i>Hylacomium splendens</i>	P		17	4	7	P	1	23	58	6	60	7	29	55				
<i>Aulacomnium palustre</i>	19	14	14	5	11	11			1	P	P	8	7					
<i>Pleurozium schreberi</i>	1		1	P	11		1	1	21	14	14		8	10				
<i>Campylium stellatum</i> *	P			P	3		P	P		8	15				18	P		
<i>Ditrichum flexicaule</i> *		P				P		1		P	P	12	3		23	P		
<i>Drepanocladus uncinatus</i>		P		12		P	P			P		1	1			P		
<i>Distichium capillaceum</i>	P	P					P	P		11						P		
<i>Sphagnum</i> spp. (2)*+	20		12		9	26			P									
<i>Drepanocladus vernicosus</i>	P				4	1	17	1										
<i>Dicranum polysetum</i>			1		3		21	14			P	P	P					
<i>Brachythecium salebrosum</i>	5	P							P		P		3	10				
<i>Ptilium crista-castrensis</i>	P	P		2		P												
<i>Calliargon giganteum</i> *							P	1				2				P		
<i>Abietinella abietina</i> *																		
<i>Polytrichum juniperinum</i>	P		P		2	1												
<i>Thuidium recognitum</i> *	P			2			P											
<i>Tortella fragilis</i> *							P											
<i>Myurella julacea</i> *	P									P					10	P		
<i>Mnium affine</i>				9					P						P			
<i>Dicranum undulatum</i>						2					P							
<i>Dicranum fuscens</i>																		
<i>Dicranum bonjeani</i>								P										
<i>Meesea uliginosa</i> *																		
<i>Mnium punctatum</i>							P											
<i>Mnium rostratum</i>																		
<i>Bryum pseudotriquetrum</i>					2													

TABLE 6. Cont'd.

GROUPS	TOMENTHYPNUM	MIXED										POTENT-	
		CHARACTER										ILLA	
STANDS	5 14	8 10	9 12	3	4 15	7	1 11	13 16	6	2			
TOTAL MOSS COVER	83 89	97 74	75 84	43 50	80 80	47 78	59 53	75 51	1				
NUMBER OF SPECIES PRESENT	15 10	7 9	10 10	14 12	7 12	9 8	9 4	7 7					
<i>Bryum stenotrichum</i>	P												
<i>Drepanocladus revolvens*</i>	1												
<i>Plagiothecium denticulatum</i>	P												
<i>Fissidens adianthoides</i>				P									
<i>Leptobryum pyriforme</i>				P									
<i>Tayloria lingulata</i>					P								
<i>Bryum creberrimum</i>													
<i>Tetraplodon angustatus</i>						P							
<i>Distichium inclinatatum*</i>									P			P	
<i>Tortula ruralis*</i>													P

- Species arranged according to Presence, in descending order
- "P" - indicates species in present but has less than 1% cover
- * - indicates that the species is a calciphyte according to Martensson (1956)
- + - the two species of *Sphagnum* are *S. warnstorffianum* and *S. fuscum*; the first is considered to be a calciphyte by Martensson.

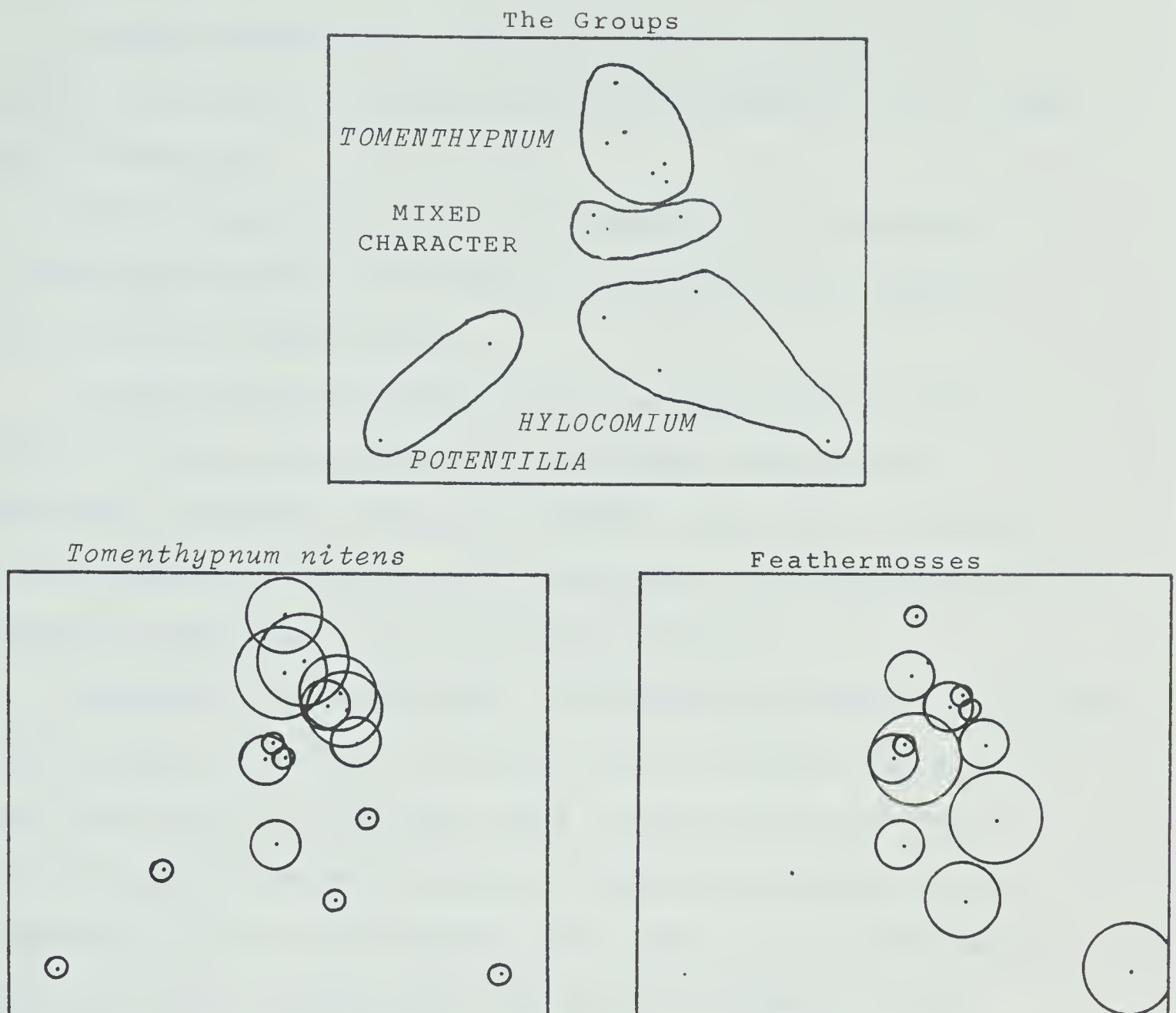
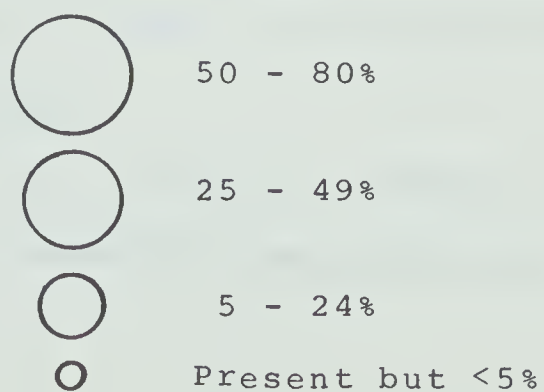


FIGURE 5. The Ordination, Showing Distribution of Cover of *Tomenthypnum nitens* and Feathermosses (*Hylocomium splendens* + *Pleurozium schreberi* + *Ptilium cristacastrensis*)



from Stand 11.

A third feathermoss, *Ptilium crista-castrensis*, is present in Stands 1, 13 and 16, but its maximum cover is only 10%, in Stand 16.

Total feathermoss cover (*H. splendens* + *P. schreberi* + *P. crista-castrensis*) is 74%, 7%, 40% and 75% in Stands 1, 11, 13 and 16 respectively.

In many respects Stand 11 has, in terms of its moss stratum, little in common with the other three stands. *Campylium stellatum*, the most abundant moss with 15% cover, shares dominance with *Tomenthypnum nitens*, *Aulacomnium palustre*, *Ditrichum flexicaule* and *Hylocomium splendens*.

Campylium stellatum and *D. flexicaule* are restricted to dry sites within the stand, *T. nitens* and *A. palustre* to moist open sites and *H. splendens* forms a very sparse and thin cover under the densest portions of the tree canopy. The abundance of the turf mosses *C. stellatum* and *D. flexicaule* makes the moss stratum much like that of Stand 6 of the *POTENTILLA* Group, although the vascular flora and development of the tree strata are quite different in the two stands.

The MIXED CHARACTER Group (Stands 3, 4, 15, 7)

I can make few general statements about the moss stratum of this group, due to the relatively non-homogeneous nature of each stand and of the group as a whole. Each stand will, therefore, be discussed separately.

Total moss cover in Stand 3 is only 43%. Although 14 species are recorded, only two, *Brachythecium salebrosum*

and *Drepanocladus vernicosus*, are abundant. The two species account for 38% cover. Both species are fairly well restricted to the flat-bottomed, damp-to-wet depressions. These depressions are periodically flooded and are exposed to relatively high light intensities, as they are not occupied by trees. The hummocks, which are densely occupied by black spruce, have relatively little moss cover.

Total moss cover in Stand 4 (adjacent to Stand 3) is also low - 50%. One end of this stand has a carpet of *Hylocomium splendens* and is similar in physiognomy, floristics and microtopography to the wetter stands of the *HYLOCOMIUM* Group. The opposite end is similar to Stand 3, although microtopography is not as pronounced. *Brachythecium salebrosum* and *Tomenthypnum nitens* are the dominants in this portion of the stand.

Moss Cover is 47% in Stand 7, which is located on an ecotone between a *Tomenthypnum*-type muskeg community on one side and an upland *Hylocomium* forest on the other. One portion of the stand is similar to Stand 11 in respect to its moss layer, in which the turf mosses *Campylium stellatum* and *Distichium capillaceum* occupy exposed, relatively dry soil under openings in the tree canopy while *Pleurozium schreberi* and *Hylocomium splendens* form a thin patchy mat under the densest portions of the pine-spruce overstory. *Tomenthypnum nitens* is restricted to the most open and moist portions of the stand.

The moss stratum of Stand 15 is very well-developed,

in contrast to those of the other stands of this Group. Total moss cover is 80%. *Hylocomium splendens* and *Pleurozium schreberi* together account for 79% cover.

Stand 15 is composed of a mosaic of two quite different types of tree strata. Some portions of the stand have a well-developed canopy dominated by pine and spruce while others are open, with very low tree density and no tree canopy. The most interesting feature of the stand is that feathermoss dominates the moss stratum of both portions of the stand and is growing rapidly in the open areas. Feathermosses characteristically are associated with low light intensities. The open areas of the stand support a well-developed shrub stratum of *Ledum groenlandicum* which may be providing the necessary shade to the feathermosses. Also, the stand is located on the east flank of a mountain. The diurnal duration of high light intensity is probably short relative to the other 15 stands, most of which are either located in valley bottoms or in depressions or level spots on west-facing slopes. The distribution of feathermoss relative to aspect exposure to light merits further study.

The POTENTILLA Group (Stands 6, 2)

These two stands, otherwise so similar, differ greatly in terms of moss cover. Stand 6 has 51% cover while Stand 2 has only 1%.

The absence of moss from Stand 2 is no doubt a function of many factors but the superficial aridity of the soil and the high degree of soil disturbance due to frost-heaving, sun-

cracking and the frequent passage of ungulates through the stand are probably the most important. Those turf mosses that are present are largely restricted to soil immediately adjacent to tree trunks. In place of a moss carpet, there is a mat of *Arctostaphylos uva-ursi* and *Dryas integrifolia* in many parts of the stand.

The vegetation of Stand 6 is not exposed to quite the extremes of environment. A tall forest borders the west and south sides of the stand; total diurnal light intensity is considerably less than in Stand 2, which is exposed to the mid-summer sun along its entire southern flank. As a result, soil moisture conditions are less extreme than in Stand 2, although still falling in the "dry" part of the spectrum. Also, the tree stratum is better developed in Stand 6. The turf mosses *Ditrichum flexicaule*, *Campylium stellatum* and *Tortella fragilis* dominate the moss stratum. Their greatest cover is near the bases of the black spruce.

X. THE SUBORDINATE VASCULAR STRATA

A. Introduction

A total of 119 subordinate vascular species (*i.e.* maturing in the "herb-dwarf shrub" and "medium shrub" strata) were identified in the 16 stands. The complete list is given in Appendix D.

Cover and frequency data for 68 of these species are given in Tables 7 and 8. Each of these species was present in at least 4 stands or had at least 5% cover in any single stand.

The mean numbers of subordinate vascular species found in the *TOMENTYPNUM*, MIXED CHARACTER, *HYLOCOMIUM* and *POTENTILLA* Groups are 36, 48, 37 and 50 respectively. The mean for the 16 stands is 41. The subordinate vascular strata are species-rich. La Roi (1967) obtained a mean of 32 species from analogous strata of 26 sample black spruce stands from the North American taiga. The figure for Jasper and Banff is almost certainly significantly greater.

The overall floristic richness of the black spruce vegetation is probably in large part a reflection of the relatively eutrophic nutrient status of the stands. Within each of the 4 Groups, however, species diversity appears to bear a close relationship to stand homogeneity. It is significant that Stand 7, which is the least homogeneous of the 16, contains the greatest number of subordinate vascular species (65), while Stand 16, the most uniform laterally in terms of both soil and tree stratum, contains the least (23).

TABLE 7. Percent Vertical Cover of Species of Subordinate Vascular Strata⁺

	GROUPS	TOMENTHYPNUM										MIXED CHARACTER										HYLOCOMIUM										POTENT- ILLA	PRESENCE NO. OF STANDS
		5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2																
Total No. of Subordinate																																	
Vascular Species		40	28	40	31	51	28	53	42	34	65	39	45	40	23	59	42																
A. Medium Shrub Species																																	
<i>Salix</i> spp. (2)*		8	24	3	19	P	23	17	10	2	5	4	7	4		7	2											15					
<i>Potentilla fruticosa</i>		P	P	2	P	P	P	3	P	P	2	P	2			14	4											14					
<i>Salix glauca</i>		2	P	2	P	P	4	P	1	P	4	P	P	P		P												14					
<i>Rosa acicularis</i>		2		P	P	1	P	4	2	P	P	P	P	1		P												14					
<i>Betula glandulosa</i>		P	2	1	1	2	P	P	P	P	1	P	P			2	P											14					
<i>Ledum groenlandicum</i>		12	18	8	9	21	7	10	17	26	7			1		P												13					
<i>Shepherdia canadensis</i>					P			P	1	P	2	P	P	3		P												9					
<i>Juniperus communis</i>								P	P	2	P	P	P	P		P	1											9					
<i>Salix candida</i>						P		P								P	P											4					
Stratum COVER		24	44	16	29	24	34	34	31	30	21	4	9	9	0	23	7																
B. Herb and Dwarf Shrub Species																																	
<i>Equisetum scirpoides</i>		2	5	3	9	2	7	5	6	P	1	3	6	4		P	P											16					
<i>Elymus innovatus</i>		1		2	P	P	P	8	1	10	2	7	6	7	1	1	4											15					
<i>Linnaea borealis</i>		2		2	P	P	P	P	3	3	3	3	P	4		P	P											15					
<i>Pyrola asarifolia</i>		P	P	P	P	P		P	P	P	1	1	P	P		P	P											15					
<i>Carex vaginata</i>		14	2	37	50	18	1	36	31	18	18	9	P			P												14					
<i>Aster ciliolatus</i>		P	P	2	P	P	P	1	P		1	P	1	1		4	P											14					
<i>Equisetum variegatum</i>		P	2	3	P	6	P	P	2	P	1	P	1			P	P											14					
<i>Petasites palmatus</i>		P	P	P	2	2			P	1	1	P	3	2		P												13					
<i>Anemone parviflora</i>		P	P	P		P	P		P	P	1	P	1	1		P	P											13					
<i>Carex gynocrates</i>		24	18	26	21	4	10	3	6	P	P		1			P												12					
<i>Equisetum arvense</i>		P		P	15	8	3	2	4	2						6	P											12					
<i>Carex concinna</i>		P				P	P	4	1		3	2	5	P		P	P											12					
<i>Rubus acaulis</i>		P	P	3	P	P		P	P		P	P	P	P		P												12					
<i>Galium boreale</i>		P		P	P			1	1	P	P	P	P	P		P	P											12					
<i>Arctostaphylos uva-ursi</i>		P					P	P	P	P	P	P	P	2		6	38											11					
<i>Juncus balticus</i>		5	4	3		7	5	3	P					P			P											11					

TABLE 7. Cont'd.

	GROUPS STANDS	TOMENTHYPNUM																MIXED CHARACTER							HYLOCOMIUM						POTENT- ILLA	PRESENCE NO. OF STANDS
		TOMENTHYPNUM																MIXED CHARACTER							HYLOCOMIUM						POTENT- ILLA	
		5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2															
Total No. of Subordinate Vascular Species		40	28	40	31	51	28	53	42	34	65	39	45	40	23	59	42															
Arctostaphylos rubra		1	7	P	1	P	1	P		6	7	P	2	P			11															
Carex capillaris		P	P	P	P	P	P	P	P		2		3			5	11															
Vaccinium vitis-idaea		2	2		6	5			7	4	P	2		P	P		10															
Solidago spp. (2)*		P	1							P	P	P	P	P	1	P	10															
Cornus canadensis			P		P		P	P	5	P	P	P		1	4		9															
Campanula rotundifolia					P		P	P	P	P	P	P	P			P	9															
Carex aquatilis		19	13	1	12	8	13	2	P								8															
Carex leptalea		2	P	P		6	P	P	P		P						8															
Mitella nuda		1	P	1	2			P	P	P	P						8															
Calamagrostis spp. (2)			P		P		P	P			P	P	P	P		P	8															
Agropyron trachycaulum			P	P	P						P					P	8															
Habenaria viridis		P	1			P		P	P		P					P	8															
Parnassia montanensis				P	P	P		P	P		P		P	P			8															
Epilobium angustifolium		P		P	P	P					P	P	P	P			8															
Fragaria virginiana		P	P	P							5	P	1	P	P		8															
Viola renifolia		P	P	P	P		P	P	P		P	P				P	8															
Lonicera dioica		P		P	P			P	P			P				P	7															
Castilleja septentrionalis		P	P				P	P			P					P	7															
Antennaria pulcherrima			P				P	P			P		1	P	2	P	7															
Senecio pauperculus				P		P		P			P		P	P			7															
Zygadenus elegans			P							P	2					P	6															
Geocaulon lividum						P			1	P	P	P				P	6															
Habenaria obtusata					P	P			P		P	P		P			6															
Orchis rotundifolia								P	P	P	P	P					6															
Carex scirpoidea								P	P						14	5	5															
Achillea millefolium					P		P						1	P			5															
Tofieldia glutinosa						P					P	P			1	P	5															
Polygonum viviparum			P			1							P		P	P	5															

TABLE 7. cont'd.

Total No. of Subordinate Vascular Species	GROUPS		MIXED CHARACTER										HYLOCOMIUM				POTENTILLA				PRESENCE	
STANDS	TOMENTHYPNUM		CHARACTER										ILLA				NO. OF STANDS					
	5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2						
40 28 40 31 51 28 53 42 34 65 39 45 40 23 59 42	5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2						
<i>Pyrola secunda</i>		P			P						P		P	P								
<i>Oxycoccus microcarpus</i>	5		P		6	3						2										
<i>Carex rostrata</i>	3				P					1					P							
<i>Mertensia paniculata</i>				P		P						P	2									
<i>Carex aurea</i>	P						P					P			2							
<i>Scirpus pumilus</i>							P								3	P						
<i>Carex flava</i>	P						P			P		P			P							
<i>Pedicularis groenlandica</i>		P	P		P					P												
<i>Astragalus frigida</i>					P	P						P	P									
<i>Vaccinium caespitosum</i>										P			1	P								
<i>Hedysarum alpinum</i>													5	3	P							
<i>Dryas integrifolia</i>																						
Summed COVER	80	46	93	111	75	47	65	68	44	49	27	39	28	24	39	52						

+ - only those species are presented which had a cover of at least 5% in any stand, or were present in at least 4 stands; the remaining species, and the stands in which they occurred, are included in Appendix D.

* - *Salix* spp. (2) = *S. mackenziana* + *S. myrtillofolia* and morphological intermediates.
Solidago spp (2) = *S. decumbens* + *S. multiradiata* (believe *S. multiradiata* most abundant).

Calamagrostis spp. (2) = *C. inexpansa* + *C. canadensis* (believe most individuals were *C. inexpansa*).

"P" = present in stand but cover less than 1%.

Inspection of Tables 7 and 8 will show that the 4 Groups differ much less in species composition than they do in vegetation structure. There are few species which show complete fidelity to a single Group.

B. The TOMENTYPNUM Group (Stands 5, 14, 8, 10, 9, 12)

The medium shrub stratum is well-developed in all stands of the Group. Stratum cover (see Table 7) ranges between 16% and 44%, averaging 29%. The stratum is dominated by *Ledum groenlandicum* and a morphological aggregate of *Salix* species, the prime components of which are *S. myrtillofolia* and *S. mackenzieana*. The height of the shrubs averages about 0.5 m.

The dispersion pattern of the dominant shrubs is highly contagious, reflecting the hummock-hollow microtopography. *Ledum* is restricted to the tops and sides of the hummocks; most of the *Salix* also conforms to this pattern, though a few individuals occupy damp hollows as well.

Potentilla fruticosa, *Salix glauca*, and *Betula glandulosa* occur in all 6 stands but are relatively unimportant in terms of cover. Though most individuals belonging to these species are found on the hummocks, their distribution is not as rigidly controlled as that of *Ledum*. *Potentilla fruticosa* and *Betula glandulosa* in particular seem to tolerate very damp soil. Scattered individuals of these species are commonly present on floating sedge mats bordering small lakes in the Jasper Park lowlands. Though it appears to have a much broader moisture tolerance than *Ledum groenlandicum*,

P. fruticosa seem highly intolerant of shade.

Much of the *Salix* has been subjected to occasional browsing, presumably by moose. The browsing has promoted the proliferation of branches and appears, in some stands, to have caused a greater *Salix* cover than would otherwise be the case.

The herb-dwarf shrub stratum is also well-developed in all 6 stands. Stratum cover data are not available but the summed vertical covers of all herb and dwarf shrub species in each stand are presented in Table 7. Summed cover averages 79% over the Group, ranging between 45% and 140%. Members of the genus *Carex* dominate this stratum in each stand. The most abundant sedges are *C. vaginata*, *C. gynocrates* and *C. aquatilis*. The first two occupy the moist tops and sides of the moss hummocks. Though they occupy hollows as well, they avoid very damp ones or those which contain standing water for a large portion of the growing season. *C. aquatilis*, in contrast, attains greatest abundance in small pools of standing water. Its greatest estimated cover (19%) was in the wet hollows of Stand 5, which it shares with *C. rostrata*. *C. aquatilis* is also a frequent herb of the moist hummocks.

C. leptalea, though relatively unimportant in terms of cover, may be a good indicator of average soil moisture conditions. This species is rarely found far removed from the water table and is especially abundant around the margins of pools of standing water. Its abundance in a stand

TABLE 8. Percent Frequency of Species of Subordinate Vascular Strata*

GROUPS	TOMENTHYPNUM										MIXED				HYLOCOMIUM						POTENT- ILLA		PRESENCE
	STANDS	5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2						
A. Medium Shrub Species																							
<i>Salix</i> spp (2)*	82	98	72	96	20	94	88	72	40	50	72	98	40	74	52	15							
<i>Potentilla fruticosa</i>	26	6	18	6	4	P	58	6	2	34	2	36		98	96	14							
<i>Salix glauca</i>	20	14	48	2	14	40	30	16	6	42	10	18	16	12		14							
<i>Rosa acicularis</i>	58		20	22	26	4	88	82	20	14	38	46	16	8	38	14							
<i>Betula glandulosa</i>	20	62	36	P	42	16	4	16	16	18	8	34		40	22	14							
<i>Ledum groenlandicum</i>	88	78	90	66	98	62	80	100	100	62			10	4	16	13							
<i>Shepherdia canadensis</i>				P			8	2	4	24	2	30	38	6		9							
<i>Juniperus communis</i>							P	8	10	28	6	P	2	8	46	9							
<i>Salix candida</i>						P	P							6	10	4							
B. Herb and Dwarf Shrub Species																							
<i>Equisetum scirpoides</i>	84	98	82	90	80	94	84	100	16	60	66	90	82	100	6	P	16						
<i>Elymus innovatus</i>	12		38	10	16	16	82	24	96	44	100	74	96	40	56	78	15						
<i>Linnaea borealis</i>	42		74	2	18	2	40	100	66	42	72	2	76	46	14	P	15						
<i>Pyrola asarifolia</i>	32	6	32	2	32		30	16	46	66	58	28	18	P	36	30	15						
<i>Carex vaginata</i>	74	28	100	98	90	P	96	100	94	82	82	18		P	6	14	14						
<i>Aster ciliolatus</i>	14	2	48	8	6	6	62	28	44	60	14	60	28		78	90	14						
<i>Equisetum variegatum</i>	62	42	100	P	96	20	36	68	28	68	12	38		8	58	14	14						
<i>Petasites palmatus</i>	2	8	4	26	52			12	52	26	66	64	58	8	P	13	13						
<i>Anemone parviflora</i>	P	6	28		4	6		P	12	80	50	34	4	50	66	13	13						
<i>Carex gynocrates</i>	96	100	98	98	78	96	86	72	6	22		12		4		12	12						
<i>Equisetum arvense</i>	12		24	92	96	74	94	90	60	18	8			70	2	12	12						
<i>Carex concinna</i>	P				6	6	40	34	64		44	80	50	8	66	4	12						
<i>Rubus acaulis</i>	28	6	74	58	46		10	4		20	32	28	22	2		12	12						
<i>Galium boreale</i>	14		64	4			72	66	6	46	42	48	22	44	54	12	12						
<i>Arctostaphylos uva-ursi</i>	2					2	20	6	P	8	14	16	20	86	100	11	11						
<i>Juncus balticus</i>	38	34	72		90	26	98	22			32	2		2	2	11	11						
<i>Arctostaphylos rubra</i>		16	50	P	10	P			62	68	38	20	2	2		11	11						
<i>Carex capillaris</i>		6	2	P	6	2	6	8	36		20			46	2	11	11						
<i>Vaccinium vitis-idaea</i>	32		94		82	72		78	94	40	20		10	2		10	10						

TABLE 8. cont'd.

GROUPS	TOMENTHYPNUM								MIXED				HYLOCOMIUM						POTENT- ILLA			PRESENCE
STANDS	5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2	1	11	13	16	6	2
<i>Solidago</i> spp. (2) *	4		38						2	64	2	2	24	2	50	P						10
<i>Cornus canadensis</i>			34		10		2	96	22	20	12		34	52								9
<i>Campanula rotundifolia</i>					P		4	4	16	10	32	4			48	8						9
<i>Carex aquatilis</i>	94	100	32	96	78	78	2	44														8
<i>Carex leptalea</i>	28	2	P		60	P	10	P		2												8
<i>Mitella nuda</i>	60	2	62	70			4	30	6	6												8
<i>Calamagrostis</i> spp. (2) *		8			16		4		2				4	P	80	46						8
<i>Agropyron trachycaulum</i>		2	4	P					P				P		26	28						8
<i>Habenaria viridis</i>	4	42			10		4	2	4						6	4						8
<i>Parnassia montanensis</i>			P	2	8		P		P				6	6	P							8
<i>Epilobium angustifolium</i>	22		P	6	6					6		4	38	2								8
<i>Fragaria virginiana</i>	2		18						54		2	42	42	P	8							8
<i>Viola renifolia</i>	2		26		P		4	18	40		6				P							8
<i>Lonicera dioica</i>	4		2	2			26	6			P				2							7
<i>Castilleja septentrionalis</i>	P	4				4	P		10						10	26						7
<i>Antennaria pulcherrima</i>		4					6		14		36	P			78	90						7
<i>Senecio pauperculus</i>			4		2		10		10		2	2			64							7
<i>Zygadenus elegans</i>		4					4		2	56					6	10						6
<i>Geocaulon lividum</i>					10			36	38	P	32				2							6
<i>Habenaria obtusata</i>				2	2			4	2		6		12									6
<i>Orchis rotundifolia</i>							P	20	2	14	P				14							6
<i>Carex scirpoides</i>			P				P	P							94	100						5
<i>Achillea millefolium</i>				4		4					26	32	32									5
<i>Tofieldia glutinosa</i>		6			2				P		10				54	56						5
<i>Polygonum viviparum</i>					8							2			2	6						5
<i>Pyrola secunda</i>		2			22						P		4	50								5
<i>Oxycoccus microcarpus</i>	44		16		56	30						P										5
<i>Carex rostrata</i>	58				P				10						2							4
<i>Mertensia paniculata</i>			34			6			P			24	42									4

TABLE 8. cont'd.

GROUPS STANDS	TOMENTHYPNUM										MIXED CHARACTER				HYLOCOMIUM						POTENT- ILLA		PRESENCE
	5	14	8	10	9	12	3	4	15	7	1	11	13	16	6	2							
<i>Carex aurea</i>	8						2					2			22		4						
<i>Scirpus pumilus</i>							2			P					32	70	4						
<i>Carex flava</i>	P									P		P			2		4						
<i>Pedicularis groen- landica</i>		2	P	10						20							4						
<i>Astragalus frigida</i>				8		4						8	6				4						
<i>Vaccinium caespitosum</i>										2	2		26	10			4						
<i>Hedysarum alpinum</i>												68	40		22		3						
<i>Dryas integrifolia</i>																50	1						

* - see Footnotes accompanying Table 7.

"p" = present in stand but was not found in any of the 50 1x1 m quadrats used in frequency tabulation.

probably indicates that a high water table is a normal phenomenon.

There are some floristic differences between the vegetation of the *Sphagnum* and *Tomenthypnum* hummocks. *Oxycoccus microcarpus*, and, to a lesser extent, *Vaccinium vitis-idaea*, are associated with *Sphagnum fuscum*. *Ledum groenlandicum*, *Betula glandulosa*, *Juncus balticus*, and *Carex gynocrates* appear to show no preference for either substrate. The majority of the remaining shrubs and herbs appear to favour the *Tomenthypnum* hummocks, thus the *Sphagnum* usually bears less vascular vegetation and always fewer species.

Elymus innovatus, *Linnaea borealis*, *Aster ciliolatus*, *Pyrola asorifolia*, *Equisetum scirpoides* and *E. variegatum* are most abundant in the drier portions of the stands.

Equisetum arvense, *Rubus acaulis*, *Arctostaphylos rubra* and *Carex capillaris* attain peak abundance in moist to damp depressions, in which mineral soil is near the surface.

The apparent moisture preferences of many of the herbs and shrubs may in fact be a manifestation of a preference for lime-rich conditions, but this hypothesis cannot be tested with my data.

C. The HYLOCOMIUM Group (Stands 1, 11, 13, 16)

The subordinate vascular strata of these stands are much less prominent than those of the *TOMENTHYPNUM* stands.

Though species diversity is as great and many species occur in both Groups, the medium shrub stratum has much less cover than in the *TOMENTHYPNUM* stands. This appears

to be largely a reflection of lower light intensity in the *HYLOCOMIUM* stands. Stand 16, the darkest, has no shrub stratum. The remaining 3 stands differ from the *TOMENTHYPNUM* stands in containing significant amounts of *Juniperus communis* and *Shepherdia canadensis*, species associated with mesic soils. These shrubs avoid deep shade.

The herb-dwarf shrub stratum is also not well-developed. In Stands 1 and 16, the moss stratum is much more prominent than the subordinate vascular strata. *Equisetum scirpoides*, *Elymus innovatus* and *Linnaea borealis* can withstand extreme shade, are present in each stand, and together account for much of the cover of the stratum. *Petasites palmatus*, *Pyrola asorifolia*, *Carex concinna*, *Solidago* spp., and *Fragaria virginiana* occur in all 4 stands and attain high frequency in some. However, none of the above species have a high fidelity to the *HYLOCOMIUM* Group; most are present in the *TOMENTHYPNUM* and MIXED CHARACTER stands, and achieve their greatest cover in stands of these other Groups. Only *Equisetum scirpoides*, *Linnaea borealis*, *Petasites palmatus*, *Carex concinna* and *Hedysarum alpinum* attain their greatest cover in one of the *HYLOCOMIUM* stands.

D. The *POTENTILLA* Group (Stands 6, 2)

The medium shrub stratum of both stands is conspicuous but not high in cover. A large number of medium shrub species are present, as in the other Groups, but *Potentilla fruticosa* is clearly the dominant. The height of the stratum averages about 0.75 m. Like those of the *TOMENTHYPNUM* stands,

the shrub species are contagiously distributed, most of them, including *P. fruticosa*, avoiding the hollows.

The herb-dwarf shrub stratum is also best-developed on the hummocks. In Stand 2 this stratum is overwhelmingly dominated by *Arctostaphylos uva-ursi* (38% cover), a mat-forming species which is a good indicator of dry surface soil. *Dryas integrifolia* another prostrate shrub, is also abundant in Stand 2. Stand 6 does not contain the latter species and though *A. uva-ursi* has significant cover (6%), it does not completely dominate the stratum.

Carex scirpoidea has very high frequency in both stands. In Stand 6, with 14% cover, it dominates the herb-dwarf shrub stratum.

Antennaria pulcherrima, *Tofieldia glutinosa*, *Scirpus pumilus*, *Calamagrostis* spp., *Agropyron trachycaulum*, *Castilleja septentrionalis* and *Aster ciliolatus* all attain their greatest frequencies in the two *POTENTILLA* stands, but the cover of none of them exceeds 5%, partly due to their more-or-less erect growth form and sparse foliage. All of these species exhibit a preference for the hummocks.

The hollows of Stand 6 are larger, more flat-bottomed and more moist than those of Stand 2. These moist hollows support populations of *Carex capillaris*, *C. aurea* and *C. flava* - all of which appear to have a preference for moist, heavy mineral soil and high light intensity.

E. The MIXED CHARACTER Group (Stands 3, 4, 15, 7)

As this is a non-homogeneous Group, few general

statements can be made as to the nature of the shrub and herb populations.

As with the tree stratum, soils and moss stratum, the subordinate vascular strata represent a mixture of *TOMENTHYPNUM* Group and *HYLOCOMIUM* Group characteristics. In areas of each stand in which the tree stratum is particularly well-developed, the medium shrub and herb-dwarf shrub strata are poorly developed; the converse being equally true.

Each of the stands contains at least 8 medium shrub species. The dominants in all stands are *Salix* and *Ledum groenlandicum*, as in the *TOMENTHYPNUM* stands, but *Shepherdia canadensis* and *Juniperus communis*, present in all 4 stands, assert a relationship with the *HYLOCOMIUM* Group. The average cover of the medium shrub stratum is 29%. On the whole, it is much better developed than in the *HYLOCOMIUM* Group.

Carex vaginata is the cover-dominant of the herb-dwarf shrub stratum in all 4 stands. *C. gynocrates*, although present in each stand, is much less important than in the *TOMENTHYPNUM* Group. *C. aquatilis* is present in 2 stands but is relatively unimportant.

The herb-dwarf shrub stratum is as well-developed as in the *TOMENTHYPNUM* Group - summed cover ranges between 44% and 68%, averaging 56%.

Equisetum scirpoides, *Elymus innovatus*, *Linnaea borealis*, and *Equisetum arvense* occupy all 4 stands and together make an important contribution to cover in each of them. *Pyrola asarifolia*, *Equisetum variegatum*, *Galium boreale*,

Arctostaphylos uva-ursi, *Cornus canadensis*, *Campanula rotundifolia*, *Mitella nuda*, and *Orchis rotundifolia* are present in all 4 stands but none of them have high fidelity to the Group.

F. Performance on the Ordination of Species with High Prominence Values

The prominence values of 10 species (those that attained a prominence value of 75 or more in at least one stand) are plotted on the ordination in Figure 6. These species, because of their great prominence, have had a marked controlling effect on the distribution of stands in the ordination, an effect which is merely modified by less important species.

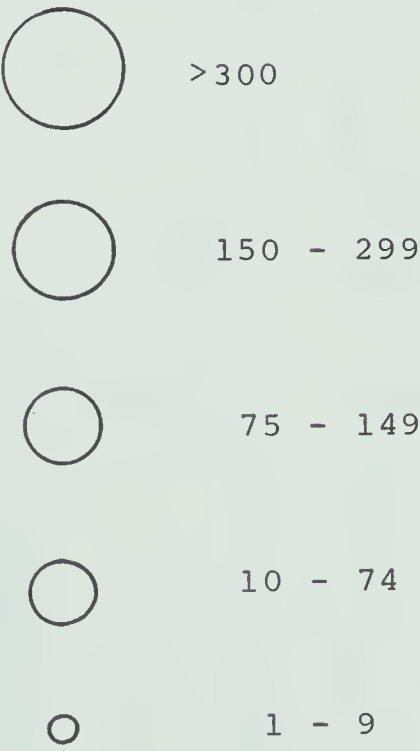
It is significant that not one of the 10 species is restricted to a single Group. Most of them, however, attain greatest prominence in a specific area of the ordination.

The *POTENTILLA* stands have been segregated from the rest by *Potentilla fruticosa*, *Carex scirpoidea* and *Arctostaphylos uva-ursi*, all of which attain their peak prominence in these two stands. *A. uva-ursi* is especially significant in that it is largely responsible for the isolation of Stand 2.

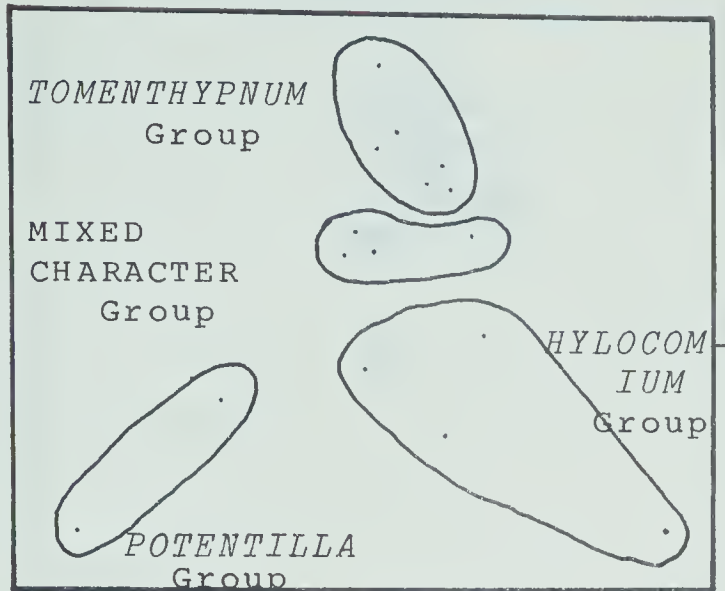
Ledum groenlandicum, *Carex vaginata*, *C. gynocrates* and *C. aquatilis* have segregated out the *TOMENTHYPNUM* and MIXED CHARACTER stands from the *HYLOCOMIUM* and *POTENTILLA* Groups. *C. vaginata* and *Ledum groenlandicum* form a bond between the *TOMENTHYPNUM* and MIXED CHARACTER Groups while *C. gynocrates* and *C. aquatilis* attain peak abundance in the *TOMENTHYPNUM* Group, thus introducing a degree of separation.

Equisetum arvense appears responsible for the "right-

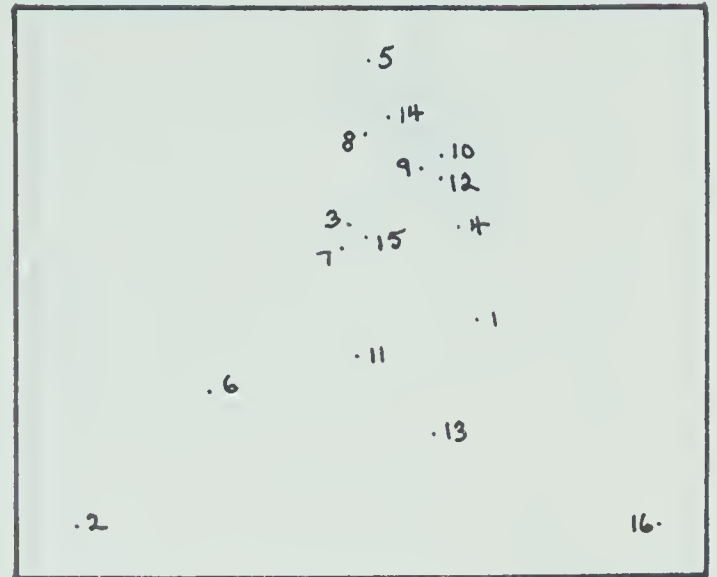
FIGURE 6. The Ordination, Showing Distribution of Prominence Values of the Ten Most Prominent Subordinate Vascular Species.



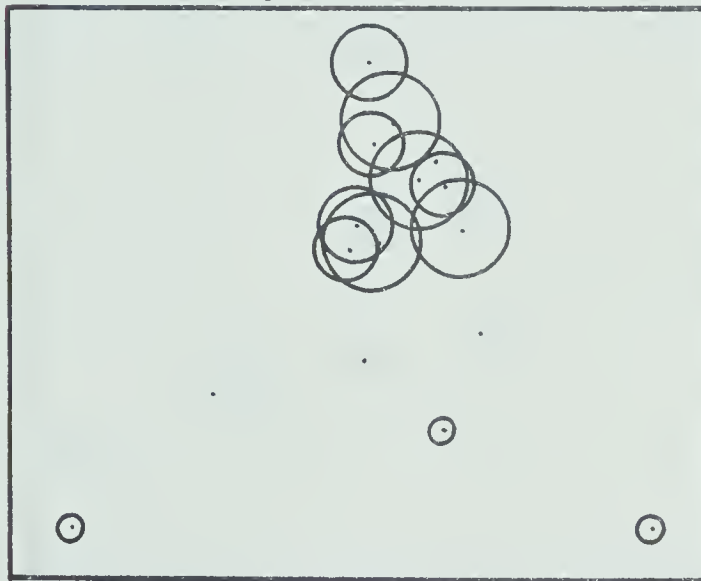
THE GROUPS



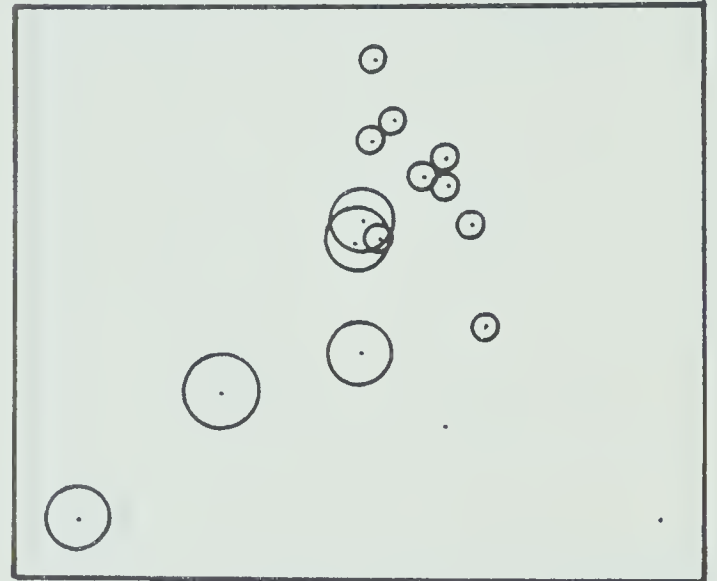
99.
THE STANDS



Ledum groenlandicum



Potentilla fruticosa



Salix spp.



Carex vaginata

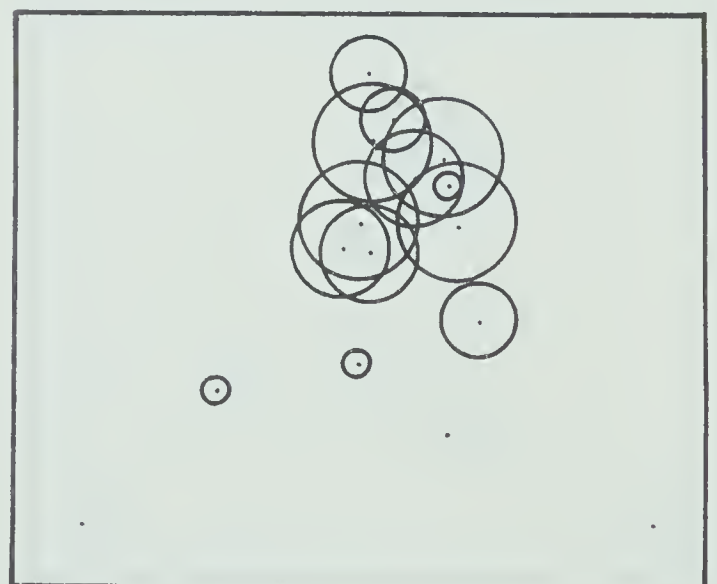


FIGURE 6

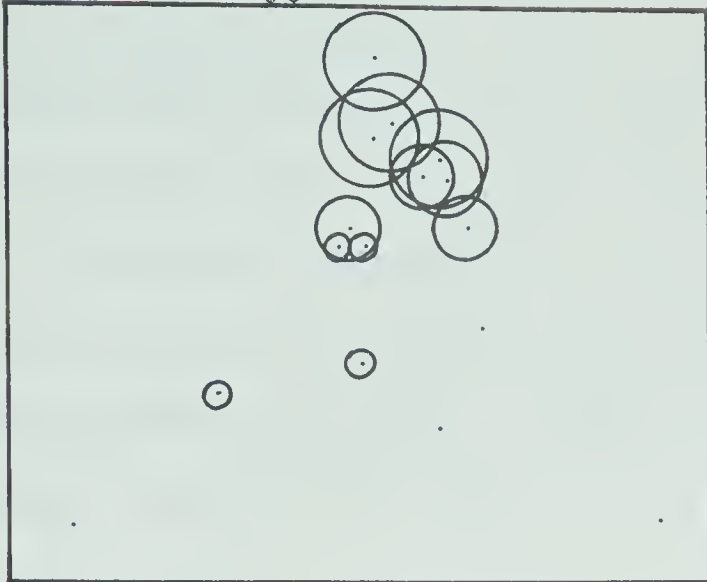
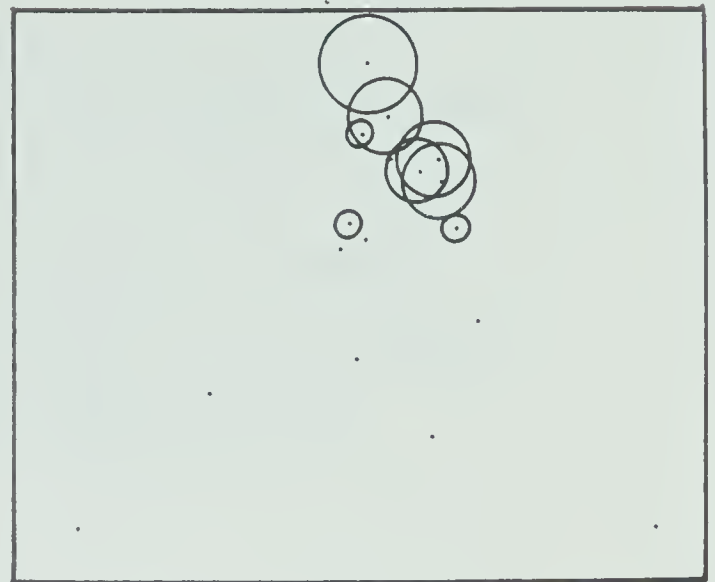
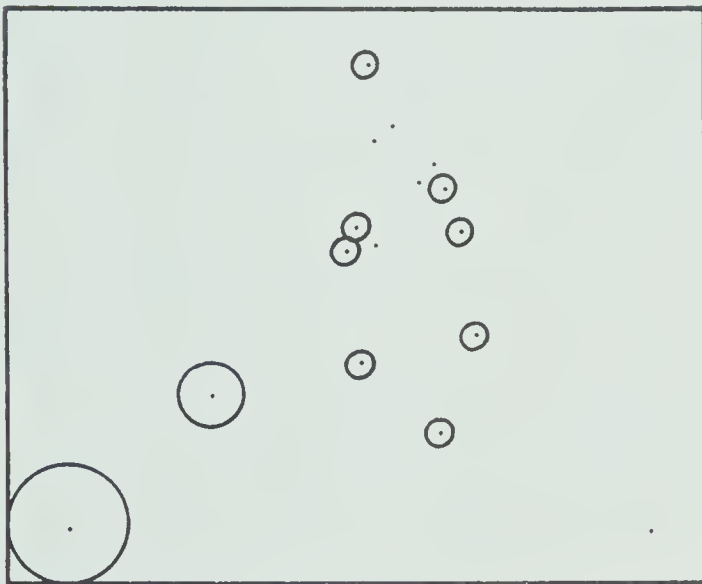
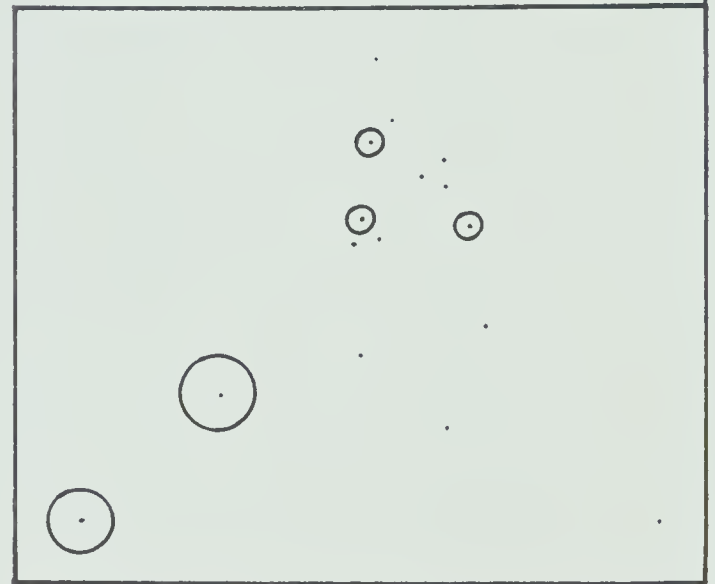
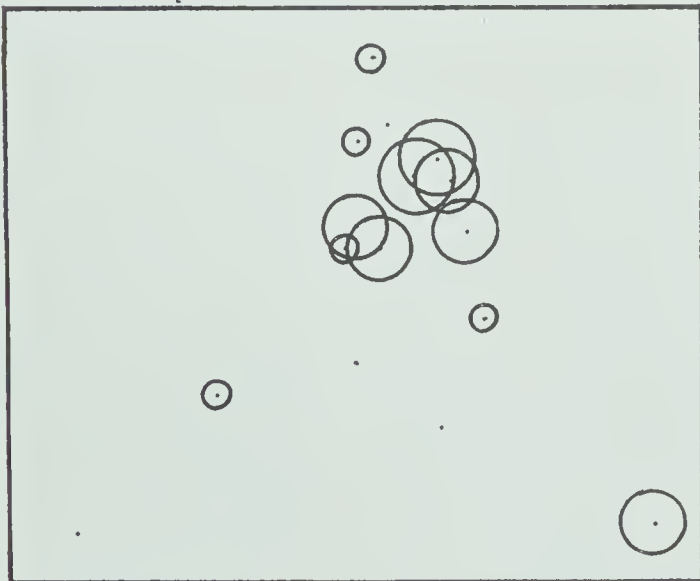
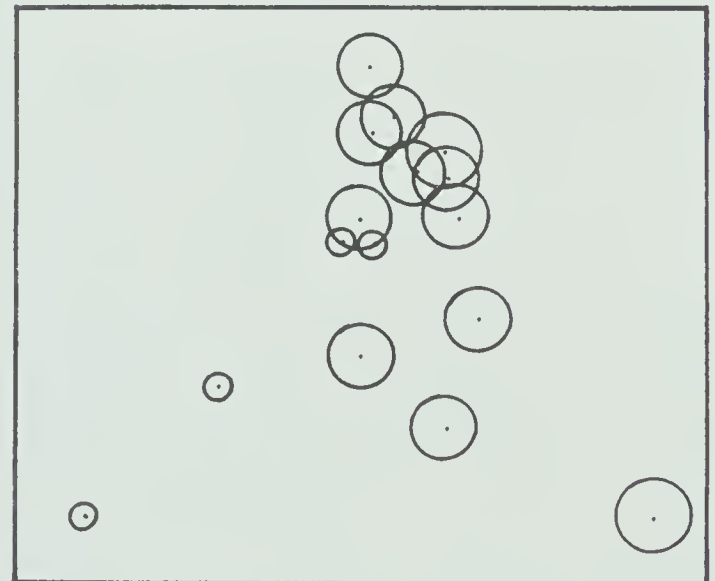
Carex gynocrates*Carex aquatilis**Arctostaphylos uva-ursi**Carex scirpoidea**Equisetum arvense**Equisetum scirpoides*

FIGURE 6 Cont'd.

left" distribution of stands. Stands 11 and 13 of the *HYLOCOMIUM* Group and Stands 6 and 2 of the *POTENTILLA* Group are somewhat separated from the remaining, moister, stands.

Equisetum scirpoides is the sole important species which appears to have had little net effect on the relative distribution of stands, though it does indicate some preference for moist soil.

XI. THE TREE STRATUM

A. The TOMENTHYPNUM Group (Stands 5, 14, 8, 10, 9, 12)

1. General Characteristics

The tree strata of the *Tomenthypnum* stands are highly similar in overall physiognomy. Total tree canopy cover ranges between 17 and 24%. The black spruce exhibits a growth form typical of relatively open peat woodland with a narrow columnar upper crown spreading at the base, with lower branches alive and touching the ground. Consequently a large portion of the cover of each tree, and thus of the stratum, is contributed by the lower meter of tree foliage.

White spruce occurs in 5 stands and lodgepole pine in 3, but black spruce is clearly the dominant in all 6 stands, as shown by the basal area, cover and density data in Table 9. Total basal area (all species summed) averages 16.3 m²/ha; that of black spruce alone accounts for over 85% of the total in each stand.

The black spruce trees are not large. Stand 10 contains the tallest - 13.7 m at 156 years. Over the 6 stands average height of the tallest individual black spruce is 9.8 m. The mean height of stems greater than 2.5 cm DBH ranges between 4.0 and 7.0 m, averaging only 5.1 m for the Group. The maximum recorded diameter is 19.3 cm, taken from the above-mentioned tallest specimen. Mean DBH of "trees" ranges from 4.6 to 7.9 cm and averages 6.4 cm.

Total tree density (number of living stems >2.5 cm DBH per 25 m²) ranges between 7.1 and 15.7 and averages 11.7

TABLE 9. Statistics Concerning Tree Strata of *TOMENTHYPNUM* Stands

(Stands arranged in order of ascending age)

		STANDS							Group Average
		14	12	5	8	9	10		
1) Age Data	Black Spruce	max. \bar{x}	49	72	85	86	139	156	
			41	58	71	76	102	55	
		S	3.0	7.7	7.2	6.3	21.3	31.0	
		V%	7.3	13.3	10.1	8.3	20.8	56.0	
	White Spruce	max.	43	P	55	124	148		
2) Vertical Cover %	Lodgepole Pine	max.			79	36	103		
	Black spruce		22	18	24	21	15	21	20
	White spruce		1	P	P		1	3	
	Lodgepole Pine			P	P	P	1		
	Total		23	18	24	21	17	24	21
3) Basal Area (m ² /ha)	Black spruce		10.6	14.7	15.6	20.7	12.0	14.3	14.7
	White spruce		0.2	P	P		0.7	6.2	
	Lodgepole Pine				0.5	0.5	1.8		
	Total		10.8	14.7	16.1	21.2	14.5	20.5	16.3
	4) Density (#stems >2.5 cm DBH/25 m ²)	Black spruce	\bar{x}	11.7	10.3	13.8	15.7	6.1	8.6
		S	6.3	4.9	5.1	3.9	5.7	5.9	
		S ² / \bar{x}	3.4	2.4	1.9	1.0	5.4	4.0	
White spruce		\bar{x}	0.3	P	0.1		0.6	2.3	
Lodgepole Pine		\bar{x}			0.2	P	0.4		
	Total	\bar{x}	12.0	10.3	14.1	15.7	7.1	10.9	11.7

TABLE 9. Cont'd.

	STANDS							GROUP AVERAGE
	14	12	5	8	9	10		
5) Height Data (m)								
Black spruce								
max.	8.2	8.8	8.8	8.5	11.0	13.7		9.8
\bar{x}	4.0	4.9	4.9	4.6	5.2	7.0		5.1
S	1.2	1.8	1.7	1.5	2.3	2.6		
V%	32	36	35	34	45	37		36.5
White spruce								
Lodgepole Pine	8.2	P	2.7		8.5	18.9		
max.			7.0	12.8				
max.								
6) Diameter Data (cm)								
Black spruce								
max.	11.2	10.9	12.5	11.4	18.3	19.3		13.9
\bar{x}	4.6	6.4	5.8	5.6	7.9	7.9		6.4
S	1.8	2.3	2.3	2.3	3.8	3.8		
V%	39	37	37	39	47	47		41.0
White spruce								
Lodgepole Pine	10.7	P	3.0		14.7	32.8		
max.			10.2	20.3				
max.								

(Table 9). Average density of black spruce alone is 11.0, reflecting the almost complete dominance of the stratum by this species. The standard deviations and variance:mean ratios of density are presented for black spruce in Table 9. According to Greig-Smith (1964) the variance:mean ratio will be unity if the distribution of individuals is random and the frequency distribution of plot density follows the Poisson curve. A ratio significantly greater than unity suggests a clumped (contagious) distribution and one less than unity indicates that a regular or uniform distribution of stems is present at the scale of the quadrat size employed.

With the exception of Stand 8 the black spruce stems exhibit a 5 x 5 m pattern of contagion. This large-scale pattern is probably related to differences in seed-bed quality at the times of inception of the incumbent populations. All 6 stands developed after fire and presumably the present tree strata were initiated by seed.

Much more easily explicable is the pattern of contagion relative to the microtopography of these stands. All tree species are restricted to the tops of the peat hummocks. The scale of this contagious dispersion pattern is approximately 1 x 1 to 2 x 2 m, and would thus not be revealed in the variance:mean ratio.

Although mean tree density is not high relative to the total area of the stands, "ecological density" (*sensu* Odum 1959) is probably near saturation level in many of them, due to the fact that a sizeable proportion of each stand (the

hollows) is evidently uninhabitable by any of the tree species. Horton and Lees (1961) present maps of root systems of black spruce relative to the distribution of hummocks and hollows in peatland. The illustrations show very clearly that the roots, as well as the stems, are highly restricted to the hummocks. Intraspecific competition for aerated soil and accessible nutrients can thus be great though absolute density is low.

2. Age and Size Distributions of Black Spruce Populations

Many features of the tree strata of the 6 stands appear to be correlated with stand age. Accordingly, the usual tabular arrangement of stands (relative to position in ordination) has been departed from and the 6 stands have been listed in order of ascending maximum age in Table 9. It is important to note that all statistics on height, diameter and age presented in this table, and those following, have been obtained from samples of "trees" (>2.5 cm DBH). Mean ages, standard deviations of age and the coefficients of variation ($V = (\text{std dev.}/\text{mean}) \times 100$) are presented for each stand. These three statistics have been obtained from a sample of 30 to 40 objectively selected black spruce trees per stand. The coefficient of variation "V" allows comparisons of the relative variability of age of the different stands. Standard deviations by themselves cannot be used in such comparisons, as the larger the mean the larger will be the standard deviation, other factors affecting variability being equal (Avery 1967; Nash 1965). The coefficient of

variation will also be employed in comparison of the relative variability of age and height, age and diameter, etc..

In each stand the oldest individual is a black spruce. "Stand age" (taken from these oldest trees) ranges between 49 years (Stand 14) and 156 years (Stand 10). There is evidence in the form of charred deadfall, or charcoal in the upper layers of soil that fire has played an important role in the development of the incumbent black spruce populations of all 6 stands. It is convenient, therefore, to divide the black spruce populations into 3 components as follows:

- 1) Pre-fire component (PF) - made up of individuals which were present before the latest fire. The surviving individuals of PF are the "wolf trees" of applied forestry jargon.
- 2) Immediate post-fire component (IPF) - composed of individuals which have become established within a short time of the passage of the latest fire. Probable origin is seed from PF.
- 3) Secondary post-fire component (SPF) - composed of individuals which have become established over a long period following establishment of IPF. This component occupies the reproductive size classes (seedlings, transgressives, saplings) and in older stands will extend into the "tree" size classes as well, where it can merge with the IPF. Origin mainly from seeds or layers produced by IPF.

Low coefficients of variation of age clearly indicate that the present populations of tree-sized individuals in the 4 youngest stands (14, 12, 5, 8) are largely IPF in composition. The PF has been completely removed from each of these stands, and the SPF is still largely confined to the reproductive size classes. However, the size distribution graphs

presented in Figure 7 indicate that IPF and SPF are merging in the lower DBH classes. These graphs can only be interpreted relative to age structure. The distribution of diameter between 2.5 and 12.7 cm in each of the 4 stands is not simply a reflection of correlated age structure. The coefficients of variation of age, diameter and height (Table 9) show that size exhibits much more relative variability than age in all stands. Intraspecific competition and microhabitat differences within stands are probably the main factors responsible for the wide size distribution of the black spruce in these 4 stands.

Stand 9, at 139 years, is considerably older than the above 4 stands (which range between 49 and 86 years). It has apparently passed through the period in which the IPF dominates the tree stratum and is now in a more mature, uneven-aged stage in which a large number of SPF are now trees. This is indicated by the larger coefficient of variation of age and the much larger variation of diameter, as IPF attains the larger size classes and SPF gradually fills in the lower..

Stand 10 differs in one important respect from the other *Tomenthypnum* stands. The oldest and largest trees present are surviving PF. Some of these individuals bear fire scars. Further evidence for this assumption lies in the large difference between age of the oldest tree (156 years) and mean age (55 years). The coefficient of variation of age is very high (56%). Also, a test using

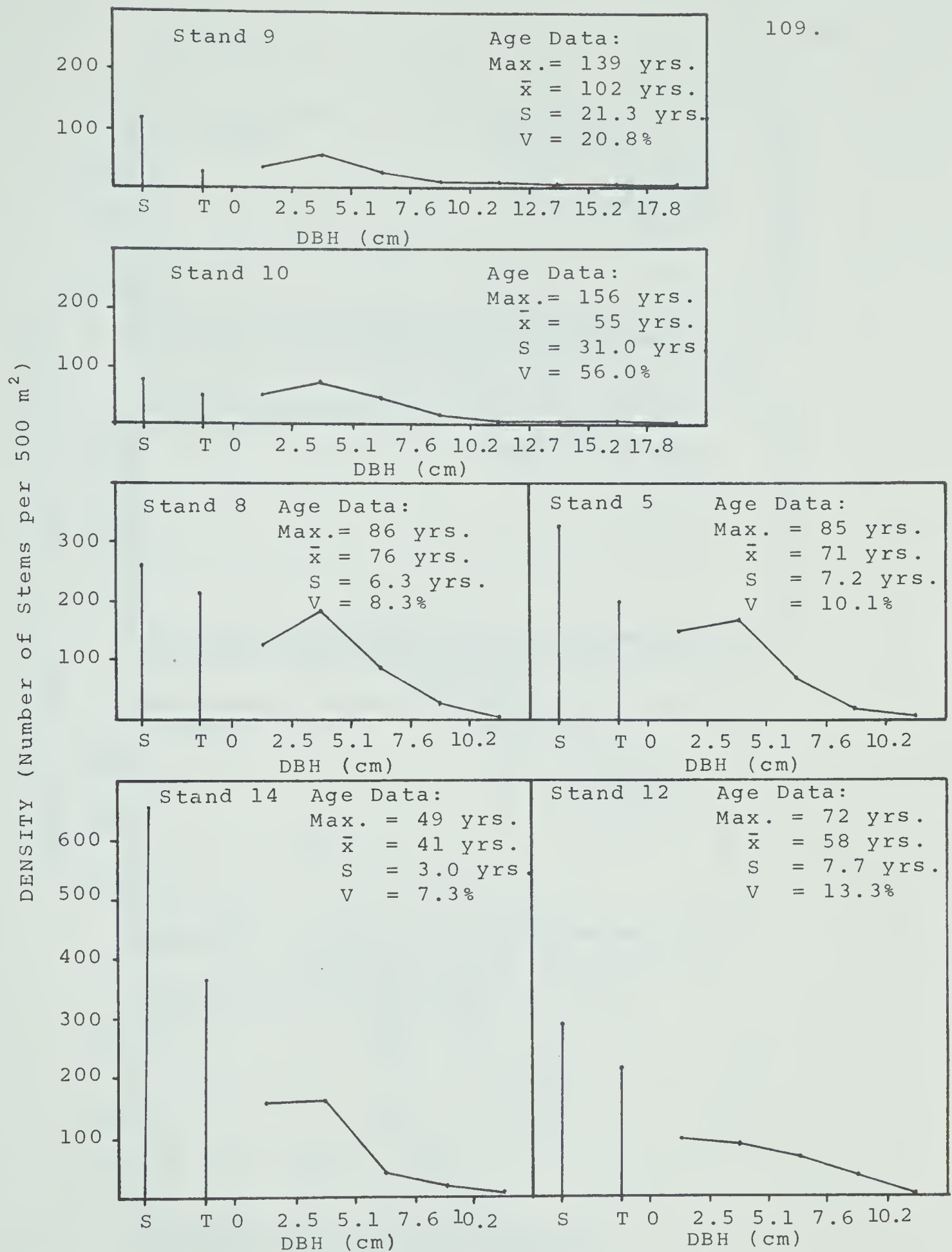


FIGURE 7. Size Distribution Graphs for Black Spruce Populations

a) Stands of the *TOMENTHYPNUM* Group

S = "seedlings" = stems <30 cm tall
 T = "transgressives" = stems >30 cm but <1.5 m tall
 DBH = diameter at breast height (1.5 m)

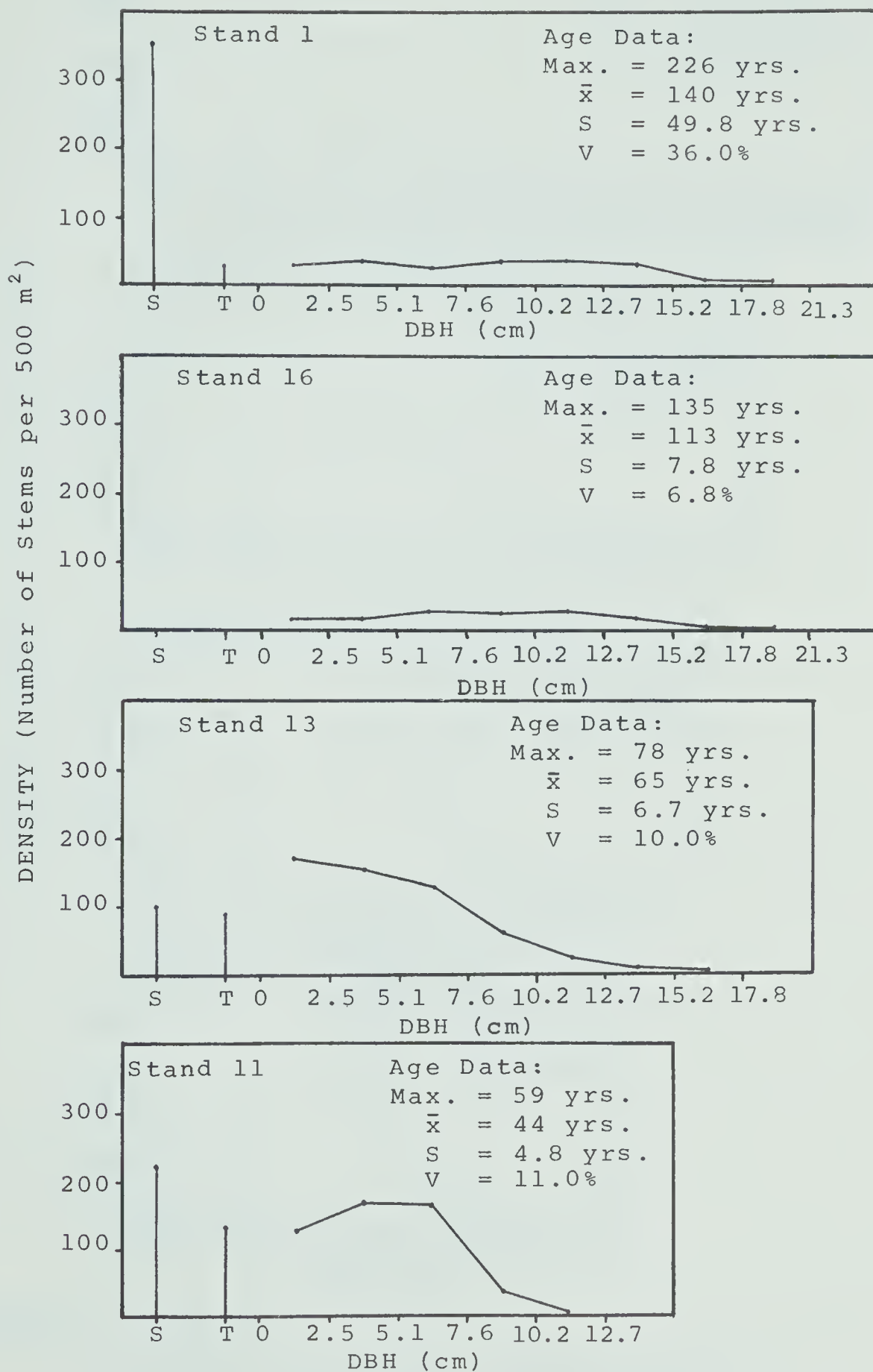


FIGURE 7. Cont'd.

b) Stands of the *HYLOCOMIUM* Group

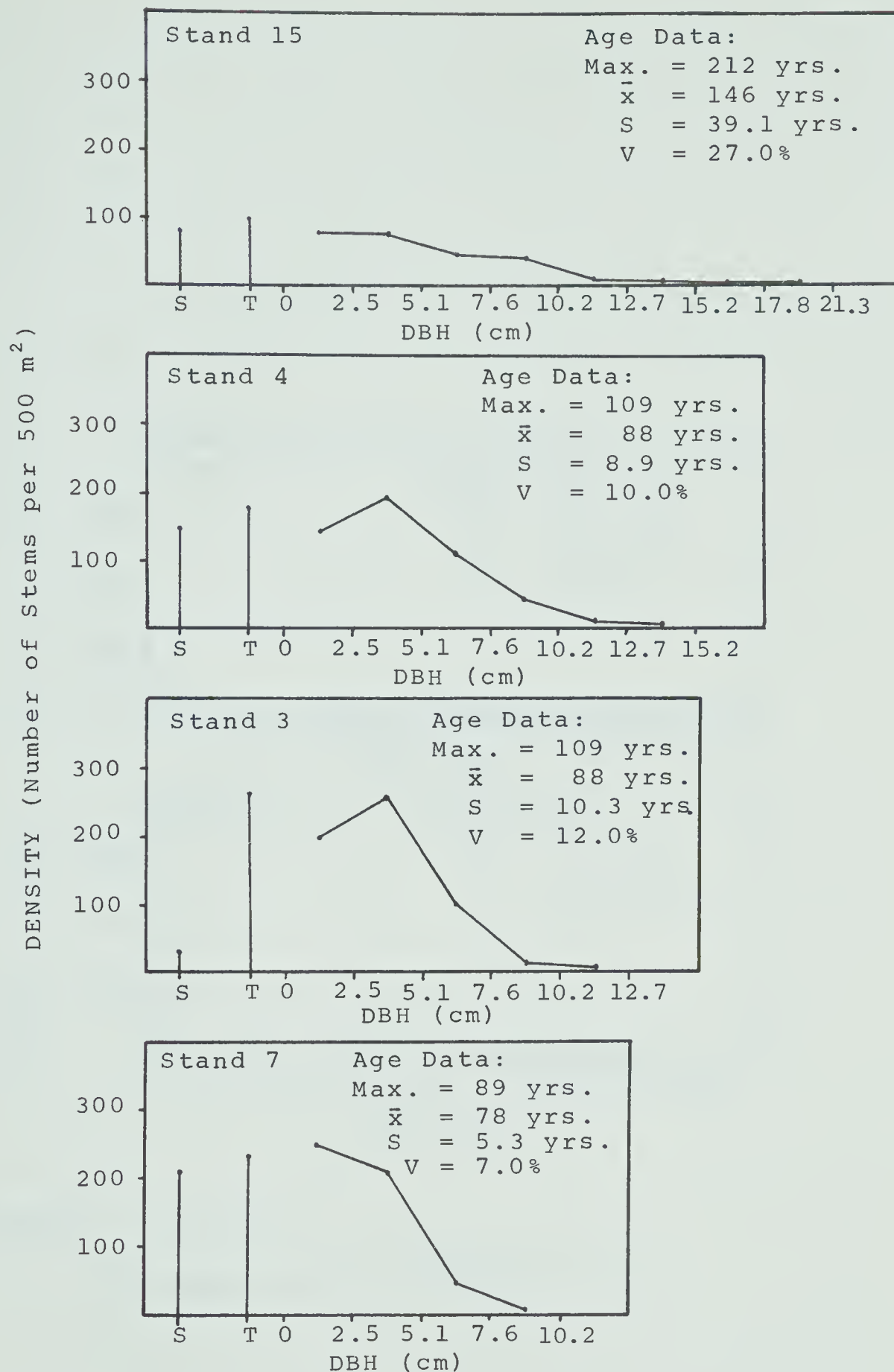


FIGURE 7. Cont'd.

c) Stands of the MIXED CHARACTER Group

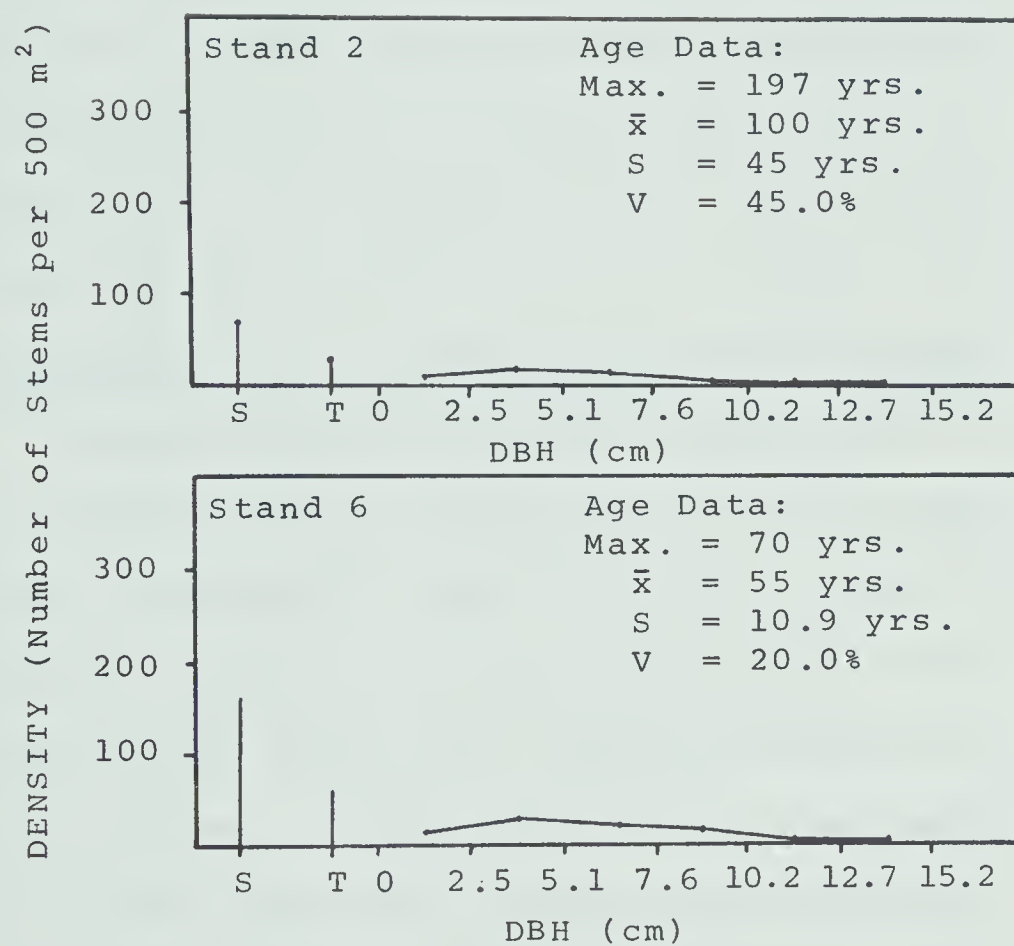


FIGURE 7. Cont'd.

d) Stands of the *POTENTILLA* Group

the standardized normal deviate (described in Nash 1965) indicates that there is less than 1% probability that the oldest tree comes from the age population from which the mean and standard deviation of age were generated.

Therefore, although the graphed diameter distribution for Stand 10 looks almost identical to that of Stand 9, the two patterns have developed quite differently. Whereas the long tail of the diameter distribution curve of Stand 10 is largely occupied by PF survivors, that of Stand 9 is largely IPF. The "hump" of the curve of Stand 10 is composed of IPF while that of Stand 9 is probably largely SPF.

3. Reproduction and Mortality of Black Spruce

Cone-bearing black spruce are abundant in all 6 stands but reproduction by seed appears to be ineffective. Field notes indicate that from 70 to 95% of the individuals occupying the reproductive size classes are of vegetative origin. *Tomenthypnum nitens*, the dominant hummock-forming moss in these stands, is apparently an excellent medium for layering but a poor medium for seedling establishment. Some true seedlings of black spruce were found on *Sphagnum fuscum* in Stands 5 and 12, but the faster-growing *S. warnstorffianum* encourages layering rather than true seedling establishment.

The most effective seedbed for black spruce seen in the 2 parks was scarified, damp mineral soil along roadsides, or on tussocks of *Polytrichum* occupying such soil.

In the *TOMENTHYPNUM* Group, successful establishment of seedlings of either seed or layer origin appears to be

confined to the tops and sides of the hummocks. Very few individuals were found in hollows and these were rarely more than a few cm tall and of seed origin. Because of their confinement to the hummocks the seedlings face severe competition from established older individuals. Possibly a layer-origin seedling has an advantage over a true seedling under such conditions, because the layer would have an appreciable head start in terms of height and food supply at the time of its rooting and establishment. Also, as layers are usually produced by the longest basal branches, their tops may project out over the hollows and receive almost full light intensity. A true seedling, in contrast, is usually shaded by the branches of older stems.

Data on seedling and transgressive density (Figure 7) suggest that reproduction decreases considerably with advanced stand age. The relationship between age and reproduction is probably not straightforward, however. So many factors, such as original site quality, relative sizes of hummocks and hollows, moisture regime, growth rates of mosses, etc. can affect the density of seedlings and transgressives that a simple linear correlation with stand age would seem unlikely.

Mortality data for black spruce are presented in Table 12, page 134. The figures refer to erect individuals only. Mortality is low relative to living stem density in all 6 stands and is virtually nil in Stands 5, 8 and 12. Stands 14 and 10, with the lowest mean ages (49 and 55 years) have the

greatest mortality in the DBH size classes (saplings and trees). In both stands the mortality is greatest in those size classes which contain the most living individuals. Mortality appears to be largely due to intraspecific competition for living space on the hummocks. There was no evidence to suggest that any of the stands had reached a state of senescence or that mortality was due to browsing animals, parasites or disease. Although approximately 40 black spruce were cored in each stand, not a single case of systemic rot at butt height was found.

4. Other Tree Species

Lodgepole pine is sparingly present in 3 of the 6 stands (Table 9). Almost all individuals present are of tree size; no seedlings or transgressives of pine were found. The pine appears to have entered the 3 stands following fire, becoming established at the same time as the IPF components of the black spruce populations.

Abundant pine seed supplies are present near every *Tomenthypnum* stand, yet not a single recently germinated pine seedling was found. This strongly suggests that the main barrier to the establishment of pine in the black spruce-dominated peatlands of the study area is the nature of the seedbed, rather than direct competition with black spruce. Once established in the peatland, the pine initially grows faster than the black spruce, though not as rapidly as the pine on adjacent upland slopes. It appears that fire, by altering the seedbed, is necessary before pine can enter the

peatland. Once established, the pine can adapt itself to the wettest soils occupied by black spruce. Establishment of pine on peatland is nevertheless a rare event in Jasper and Banff.

White spruce is present in 5 *Tomenthypnum* stands but only in Stand 10 is it abundant. The size and age distributions of white spruce in Stand 10 are similar to those of black spruce - the population evidently contains both a pre-fire and a post-fire component. Stand 10 is of the drier stands of the Group; this may account for the relative abundance of white spruce. Neither seedlings nor transgressives were found in any of the stands, though seed sources are not distant. Like the pine, white spruce may be barred from establishment in the *Tomenthypnum* stands because of seedbed unsuitability. Once established it apparently has difficulty increasing or maintaining its population size because of an inability to reproduce by vegetative means.

B. The HYLOCOMIUM Group

Preliminary Discussion

Stands 1 and 16, on the basis of soil moisture and subordinate vegetation, are more similar to each other than either is to Stands 11 and 13. Yet they are separated by Stands 11 and 13 in the ordination, constructed with subordinate vascular vegetation data. I believe that this anomaly is largely due to the fact that part of Stand 1 contained large amounts of *Carex vaginata*; this floristic feature has pulled the stand towards the *TOMENTHYPNUM* Group

and away from Stand 16. Thus far the tabular arrangement of stands has reflected their Y-axis positions in the ordination. In the following tables the arrangement of the *Hylocomium* stands will be 11, 13, 16, 1. Stands 11 and 13 are both relatively mesic to dry upland forests, in which the moss carpets are patchy. Stands 1 and 16 are moist, dark stands with well-developed moss strata and water tables near the soil surface. The new arrangement also corresponds to the order of ascending age.

It should also be noted that Stand 16 does not completely fit the selection criteria, as black spruce accounts for less than 50% of total tree density. This mistake was due to initial difficulties in distinguishing between black spruce and white x Engelmann spruce hybrids by their bark as the lower branches, which normally could provide identification criteria, were self-pruned. The error revealed itself in subsequent quantitative work, in which identification was confirmed by climbing many of the trees. I decided not to exclude the stand from the thesis as it was one of only two from Banff Park and because the relative abundance of "white" spruce in it did not seem to be associated with marked other vegetational or habitat differences.

1. General Characteristics

The general characteristics of the tree strata of the *Hylocomium* stands can be effectively shown in contrast to those of the *TOMENTHYPNUM* Group. The *Hylocomium* stands differ from the *Tomenthypnum* stands in having:

TABLE 10. Statistics Concerning Tree Strata of *HYLOCOMIUM* Stands

	STANDS				GROUP	
	11	13	16	1	AVERAGE	
1) Age Data						
Black Spruce	59 44 4.8 11 43	78 65 6.7 10 69	135 113 7.8 6 125 109 14.7 14 140 122 15.0 12	226 140 49.8 36 101		
	max. \bar{x} S V%					
White Spruce						
	max. \bar{x} S V%					
Lodgepole Pine		P		182		
	max. \bar{x} S V%					
Aspen		90				
	max.					
2) Vertical Cover %						
Black Spruce	33	32	24	36		31.3
White Spruce	5	8	4	P		
Lodgepole Pine		3	21	7		
Trembling Aspen		2				
Total	38	45	49	43		43.8
3) Basal Area (m ² /hectare)						
Black Spruce	25.3	28.9	15.0	23.7		23.3
White Spruce	2.5	2.3	15.7	0.1		
Lodgepole Pine		0.5	6.4	5.7		
Aspen		4.6				
Total	27.8	36.6	37.1	29.5		32.7
						118.

TABLE 10. Cont'd.

	STANDS				GROUP	
	11	13	16	1	AVERAGE	
4) Density (#stems >2.5 cm DBH/25 m ²)						
Black Spruce	\bar{x} 19.3 S 12.5 S^2/\bar{x} 8.1 \bar{x} 1.9	19.1 10.9 6.2 0.7 P 0.9	6.6 3.6 2.0 10.8 2.2	10.3 4.4 1.9 0.1 0.9		13.8
White Spruce						
Lodgepole Pine						
Aspen						
Total	21.2	20.7	19.6	11.3		18.2
5) Height Data (m)						
Black Spruce	max. 9.4 \bar{x} 5.5 S 1.7 V% 31	11.6 6.8 2.5 37 14.3	14.3 9.6 2.7 28 14.9 10.3 2.6 25	18.6 11.1 3.5 32 14.6		13.5 8.2 32.0
White Spruce	max. 9.8					
Lodgepole Pine						
Aspen						
6) Diameter Data (cm)						
Black Spruce	max. 12.2 \bar{x} 6.4 S 2.0 V% 31.3	15.7 7.1 3.0 42.3	19.8 10.7 3.8 35.5	17.0 11.2 3.8 33.9		16.2 8.9 35.8

TABLE 10. Cont'd.

		STANDS			GROUP AVERAGE
		11	13	16	1
White Spruce	max.	15.2	26.4	19.1	15.2
	\bar{x}			10.4	
	S			4.3	
	V%			41.4	
Lodgepole Pine	max.		P	18.5	23.4
	\bar{x}			14.0	
	S			3.3	
	V%			23.6	
Aspen	max.		16.8		

- 1) Greater importance of lodgepole pine and white spruce (cover, basal area and density data in Table 10). In addition, the upland species *Populus tremuloides* is present in Stand 13. Lodgepole pine and aspen, both shade-intolerant and initially faster-growing than black spruce or white spruce, are the tallest trees in stands where they are present.
- 2) Greater total tree canopy cover. Cover ranges between 38% and 45% and averages 41%, in contrast to the average of 21% in the *TOMENTHYPNUM* Group. The functional significance of tree cover (*e.g.* the effect on subordinate strata) is not the same as in the *Tomenthypnum* stands. Because of self-pruning of the lower branches of black spruce and other trees, cover figures are largely derived from foliage 1.5 m or more above the ground. As a result, light intensity at the medium shrub level is, for this reason alone, much less than in the *Tomenthypnum* stands.
- 3) Greater tree size. The average height of the tallest black spruce in the *HYLOCOMIUM* Group is 13.5 m, while the average is only 9.8 m in the *TOMENTHYPNUM* Group. Mean height (of black spruce >2.5 cm DBH) is 8.2 m in the *HYLOCOMIUM* Group as compared to 5.1 m in the *TOMENTHYPNUM* Group. Diameter data also show the same difference between the two Groups.

The size differences appear to be due primarily to more rapid growth rates in the *Hylocomium* stands, rather than a) to differences in age structure or b) to less relative variations in size in the *HYLOCOMIUM* Group. For example, Stands 9 and 16 are contiguous and have the same age structure; the incumbent populations of both stands developed after the same fire. The height of the tallest black spruce in Stand 9 is 11.0 m - in Stand 16 it is 14.3 m. Mean height of black spruce trees in Stand 9 is 5.2 m. In Stand 16 it is 9.6 m. It should be noted that the density of trees is much less in Stand 9 than in Stand 16 and that the black spruce has developed under a canopy of pine in Stand 16. Comparisons between Stands 12 and 13, also contiguous, show the same differences. There can be little doubt that the slower growth rates in the *Tomenthypnum* stands are a reflection of inferior edaphic conditions.

4) Greater living tree biomass per unit area.

Although direct measurements of biomass were not made, a rough estimation of the differences between the two Groups can be obtained by comparisons of data on basal area and density, knowing that tree size is considerably greater in the *HYLOCOMIUM* Group. Average total basal area in the *HYLOCOMIUM* Group is 32.7 m²/ha, while in the *TOMENTHYPNUM*

Group it is only 16.3 m²/ha. Total density averages 18.2 stems/25 m² in the *HYLOCOMIUM* Group as compared to 11.7 in the *TOMENTHYPNUM* Group.

There are two probable ecological explanations for the greater biomass in the *Hylocomium* stands:

- a) the amount of soil aeration and nutrients per area which is available to roots is much higher than in the hummock-hollow *Tomenthypnum* stands.
- b) the greater importance of other tree species would result in more efficient utilization of available habitat.

2. Age and Size Structure of Black Spruce

The stands range in age (taken from oldest tree in each stand) from 59 to 226 years. The two "upland" stands (11 and 13) are considerably younger than the two moist stands (1 and 16).

The incumbent tree populations of all 4 stands appear to have developed following fire. With the possible exception of Stand 1, there is no evidence that a living PF component is present.

The tree populations of Stands 11, 13 and 16 (aged 59, 78 and 140 years) are even-aged, as shown by their low coefficients of variation. Their size structure patterns (Figure 7) are practically identical to those of *Tomenthypnum* stands having the same age structure (compare the diameter distribution graphs of Stand 11 to Stand 14, of Stand 13 to

Stand 12 and of Stand 16 to Stand 9. Note that Stands 13 and 12 are contiguous, as are Stands 16 and 9). The only significant difference between the paired *Hylocomium* and *Tomenthypnum* stands is that there is a greater proportional amount of the populations of the *Hylocomium* stands in the larger DBH classes - a reflection of the better growth rates. It is evident that the post-fire development of tree population in both Groups is quite similar. At present, the tree strata of all the even-aged *Tomenthypnum* and *Hylocomium* stands are dominated by the IPF component.

Stand 1, at 226 years the oldest of the 16 studied; exhibits signs of senescence. Many of the larger black spruce are leaning and a number have been windthrown in the recent past. The stand is exposed to high wind speeds on its northern side (facing a lake). The resulting break-up of the PF and IPF components and the ascendancy of SPF trees is described in the age structure data (note the high coefficient of variation). The size distribution graph does not show this, however, as it is very similar to that of Stand 16. Once again it appears that black spruce age distribution patterns cannot be accurately predicted from size distribution data. The diameter distribution graph does indicate, however, that the senescence and break-up of the PF and IPF components appear to have been a very gradual process - otherwise a "bump" in lower DBH classes, due to sudden release of the SPF component, would have been expected.

3. Reproduction and Mortality of Black Spruce

Very few young stems of seed origin were seen in the

Hylocomium stands. The soil surface of the two upland stands (11 and 13) appears to provide a poor seedbed, possibly because of water deficits in dry summers. In the moist, darker stands (1 and 16) the well-developed, rankly growing feathermoss carpet appears to discourage seedling establishment. This feathermoss carpet would seem to provide ideal conditions for the production of layers. In Stand 1 young stems of layer origin are relatively abundant, especially beneath openings in the canopy provided by wind-fall. The layers originate from the lower branches of transgressives and saplings - the larger stems have divested themselves of their lower branches and thus cannot reproduce vegetatively.

Not a single stem of seedling or transgressive size was seen in Stand 16. The low light intensity and rank growth of feathermoss discourages the establishment of true seedlings, while the pruning of lower branches presents a barrier to layering. Even if layers could be produced it is doubtful if the very low light intensity would permit their survival.

Most of the mortality in the *Hylocomium* stands is in the smaller size classes and appears to be due to competition for light. A large proportion of the dead stems are clustered around larger, living trees and appear to be unsuccessful layers. Even in Stand 1, in which windthrow is taking out much of the IPF, the majority of the dead occupy smaller DBH classes. Heart rot at stump height was not found in

any black spruce - even in the oldest individuals of Stand 1.

4. Other Trees

Black spruce is the overwhelming dominant (density-wise) in Stands 11 and 13. Although some white spruce and a few lodgepole pine are present in both stands, only black spruce is reproducing successfully. Aspen is present in Stand 13 but mortality is high and most of the living stems contain heart rot. Unless alpine fir invades these stands, they will probably develop into relatively pure upland black spruce forest.

Lodgepole pine is much more abundant in Stands 1 and 16. In both stands the major part of the population occupies the larger DBH classes and is evidently IPF in origin. With the exception of one large white spruce, lodgepole pine is the sole associated tree in Stand 1. In Stand 16, however, both pine and "white" spruce (including white X Engelmann hybrids) are very important components of the tree stratum. It appears that the 3 species become established simultaneously following fire, as their age structures are almost identical. The pine population formed the initial overstory but is now, at 140 years, being superceded by spruce and is showing signs of senescence. Many of the pine have died in the fairly recent past. As neither the black nor white spruce are reproducing at present, it is difficult to predict future developments.

Eventual invasion by alpine fir seems likely in all the *Hylocomium* stands, as this species is highly shade tolerant,

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reproduces prolifically by layering, and seed sources are present near all 4 stands.

C. The *POTENTILLA* Group (Stands 6, 2)

With the exceptions of age structure and growth rates, the tree strata of the two *Potentilla* stands are very similar. Cover, basal area and density data (Table 11) clearly show that the tree strata of both stands are very poorly developed relative to those of the other Groups. Total density is only 4.5 and 2.8 stems per 25 m² in Stands 6 and 2 respectively. Canopy cover is only 13% and 15%, and the major part of these values is derived from the lower meter of tree foliage, as the black spruce has the bushy-base growth habit.

A few scattered white spruce (including a few seedlings) and a single large pine are present in Stand 2. Stand 6 contains no pine and only a single white spruce, of sapling size.

The black spruce has a contagious dispersion, being largely confined to the tops of hummocks. The size of the trees is approximately the same as in the *Tomenthypnum* stands. Mean height is 5.5 m and 4.0 m in Stands 6 and 2 respectively.

The tree strata of most *Hylocomium* and *Tomenthypnum* stands are presently dominated by clearly defined IPF black spruce populations. The *Potentilla* stands, however, have age structures that are not so clearly related to fire.

For example, Stand 6 is immediately adjacent to Stand 5, a *Tomenthypnum* stand. The incumbent black spruce

population of both stands have developed following the same fire. While post-fire establishment of black spruce appears to have been rapid in Stand 5, resulting in a clearly defined IPF population and an "even" age structure, the process of establishment appears from age data to have begun later and taken place much more gradually in Stand 6. Though the stand is younger, it has twice as much age variability as Stand 5; the term "immediate post-fire" does not apply well to the population.

As Stands 5 and 6 are so near each other, it is likely that post-fire seed supply to both was about equal. It seems, therefore, that the slow establishment in Stand 6 indicates a highly unfavourable post-fire seedbed relative to Stand 5. The possible reasons for this are no doubt numerous, but periodic soil moisture deficits and vigorous frost-heaving following removal of the vegetation cover are probably among the more important. Once established, the black spruce of Stand 6 has grown more rapidly than that of Stand 5, as indicated by height/age ratios. This may be more related to the lower density in Stand 6 and thus less intraspecific competition, than to any difference in site quality.

Stand 2 is adjacent to Stands 3 and 4. While the tree populations of Stands 3 and 4 are even aged and date from a fire of about 110 years ago, Stand 2 contains individuals which were present long before this fire. These older individuals are badly deformed and some have burn scars near

their bases. The fact that they survived the fire suggests that the stand had the same open, sparse, tree stratum before the fire as it does now. Again, as in Stand 6, post-fire establishment has been very gradual, indicating a highly unfavourable seedbed. Growth rates of the post-fire black spruce are comparable to those of Stand 6. Many of the old pre-fire survivors are smaller than individuals which are much younger. For example, an individual of age 197 years (scarred by fire) had a height of only 3.2 m and a diameter of 7.5 cm, while one aged only 51 years, located nearby, had a height of 7.0 m and a diameter of 10.0 cm. It is evident that the fire, rather than the quality of the site, is largely responsible for the very stunted growth of the older trees.

Mortality of black spruce of sapling size or greater is nil in both stands (Table 12). The figures refer only to "standing" dead but prone trunks were also rare. None of the spruce, even the most gnarled and twisted of Stand 2, showed any trace of rot at stump height.

The density of seedlings and transgressives is low, but in contrast to those of the other stands, most of them are of seed origin. Very few seedlings of height less than 10 cm were seen, and none were found which had germinated in the year prior to sampling. The heaviness of the mineral soil, its surface aridity and proneness to both frost action and sun-cracking must make seedling establishment difficult. Except for a few very small areas in each stand, the growth of moss is so slow that layering is impossible.

TABLE 11. Statistics Concerning Tree Strata of MIXED CHARACTER and *POTENTILLA* Stands

	MIXED CHARACTER				<i>POTENTILLA</i>			
	STANDS				STANDS			
	7	3	4	15	Average	6	2	Average
1) Age Data								
Black Spruce	max. 89	109	109	212		70	197	
	\bar{x} 78	88	88	146		55	100	
	S 5.3	10.3	8.9	39.1		10.9	45.0	
	V% 7	12	10	27	14	20	45	32.5
White Spruce	max. 86	98	98	129		183	67	
Lodgepole Pine								
2) Vertical Cover (%)								
Black Spruce	28	29	27	18	25.5	11	11	11
White Spruce		P				2	4	
Lodgepole Pine	8		P	4			P	
Total	36	29	27	22	28.5	13	15	14
3) Basal Area (m ² /ha)								
Black Spruce	14.8	13.2	19.6	16.2	16.0	7.9	3.0	5.5
White Spruce		0.1				0.1	1.1	
Lodgepole Pine	6.8		0.1	4.3			0.5	
Total	21.6	13.3	19.7	20.5	18.8	8.0	4.6	6.3
4) Density (#stems >2.5 cm DBH/25 m ²)								
Black Spruce	\bar{x} 13.4	18.8	18.0	9.8	15.0	4.5	2.4	3.5
	S 10.1	6.4	9.8	8.4		3.7	2.2	
	S ² / \bar{x} 7.6	2.2	13.4	7.0		3.1	2.0	
White Spruce		P				P	0.3	
Lodgepole Pine	3.1			2.1			0.1	
Total	16.5	18.8	18.0	11.9	16.3	4.5	2.8	3.7

TABLE 11. Cont'd.

	MIXED CHARACTER				POTENTILLA			
	STANDS				STANDS			
	7	3	4	15	Average	6	2	Average
5) Height Data (m)								
Black Spruce	max. 8.8	7.3	8.2	13.1	9.4	11.9	8.2	10.1
	\bar{x} 3.7	3.2	4.2	7.1	4.6	5.5	4.0	4.8
	S 1.2	1.0	1.5	2.6		2.2	1.6	
	V% 32	31	35	37	33.8	40	40	40
White Spruce	max. 14.0	3.1					8.8	
Lodgepole Pine			14.3	14.6			14.0	
6) Diameter Data (cm)								
Black Spruce	max. 12.7	11.2	12.9	16.8	13.4	15.0	13.2	14.1
	\bar{x} 4.3	4.6	5.6	7.6	5.5	6.6	5.8	6.2
	S 1.3	1.5	2.0	3.2		2.7	2.2	
	V% 30	33	36	42	35.3	41	38	39.5
White Spruce	max. 19.1	4.8					15.2	
Lodgepole Pine			23.1	14.7			30.7	

D. The MIXED CHARACTER Group (Stands 3, 4, 15, 7)

Stands 4, 15 and 7 are "mosaic communities". Their tree strata, like their soils and lesser vegetation, are laterally non-homogeneous, in some parts of the stand exhibiting *HYLOCOMIUM* Group and in others *TOMENTHYPNUM* Group characteristics. The tree stratum of Stand 3 is in almost all aspects similar to that of a *Tomenthypnum* stand, though the soil, microtopography, and lesser vegetation are somewhat different.

A comprehensive discussion of the tree strata, which in the mosaic stands would involve discussing each mosaic component separately, does not appear to be necessary as little additional insight into black spruce would be gained. Some points, listed below, deserve mention, however:

1) Though the tree stratum of each mosaic stand is physiognomically heterogenous, there is lateral homogeneity in age structure in all 4 stands; *i.e.* the black spruce from all portions of each stand belong to the same age-structure population. The younger stands (3, 4, 7) ranging from 89 to 109 years old, have even-aged tree strata, presently dominated by IPF black spruce. Stand 15, at 212 years, contains considerable numbers of SPF individuals of tree size, as indicated by the greater age variability. The 4 stands are, in terms of age structure, similar to *Hylocomium* and *Tomenthypnum* stands of the same age.

2) Reproduction by black spruce is predominantly by layering, as in the *TOMENTHYPNUM* and *HYLOCOMIUM* Groups.

3) Mortality is low in all 4 stands, and is largely confined to the smaller size classes. The only case of heart rot at stump height found during the study was observed in a 200 year old black spruce in Stand 15.

TABLE 12. Mortality Figures for Black Spruce (in Diameter Classes)

- Figures refer to dead standing stems per 500 m²

		DBH (cm)													
STAND	0- 2.5	2.5- 5.1	5.1- 7.6	7.6- 10.2	10.2- 12.7	12.7- 15.2	15.2- 17.8	17.8- 20.3	20.3- 22.9	22.9- 25.4	25.4- 27.9	27.9- 30.4	TOTALS		
TOMENTHYPNUM	5		1										1		
	14	4	10	11	4	2							31		
	8	1	1										2		
	10	6	35	13	2	2							58		
	9	4	6	0	2								12		
	12	4											4		
MIXED CHARACTER	3	3	2										5		
	4	1	4										5		
	15	17	3	4									24		
	7	4											4		
HYLOCOMIUM	1	6	25	23	17	6				1			78		
	11	4	3	2	1								10		
	13	17	4	1									22		
	16*	34	49	13	6	1							103		
POTENTILLA	6		1										1		
	2												0		

*The figures for Stand 16 represent combined mortality of white spruce and black spruce because of difficulty in distinguishing between them.

TABLE 13. Diameter Distribution of Living and Dead Stems of White Spruce, Lodgepole Pine,

and Aspen.

(expressed as # stems per 500 m²; Tallies of standing dead stems are enclosed in brackets)

		DBH (cm)														
		0-	2.5	5.1	7.6	10.2	12.7	15.2	17.8	20.3	22.9	25.4	27.9	TOTALS		
STAND		2.5	5.1	7.6	10.2	12.7	15.2	17.8	20.3	22.9	25.4	27.9				
WHITE SPRUCE																
TOMENTHYPNUM		5	1											1 (0)		
	14	6	3	1		1								11 (0)		
	10	14 (2)	21 (1)	12	7	1 (1)			2		1		1	59 (4)		
	9	3	4	4	2		1							14 (0)		
	12	1												1 (0)		
MIXED CHARACTER																
	3		1											1 (0)		
HYLOCOMIUM																
	1								1					1 (0)		
	11	31	25	8	4									68 (4)		
	13		5	(1) 2	(1) 2		(2) 1	3		1				14 (0)		
	16*	4	39	63	46	40	17	8		3				220 *		
POTENTILLA																
	6	1												1 (0)		
	2	1			3	1	1	1						7 (0)		

TABLE 13. Cont'd.

STAND		0-2.5	2.5-5.1	5.1-7.6	7.6-10.2	10.2-12.7	12.7-15.2	15.2-17.8	17.8-20.3	20.3-22.9	22.9-25.4	25.4-27.9	TOTALS
LODGEPOLE PINE													
<i>TOMENTHYPNUM</i>		5	1	1	2	1							5 (0)
		9		3 (1)		3 (1)		1					7 (2)
MIXED CHARACTER													
15		2	4 (2)	9 (3)	7	8	8	3	2				43 (5)
7		12 (7)	20	7 (1)	12 (2)	8	5	4	5 (1)	1 (1)			74 (12)
<i>HYLOCOMIUM</i>		1			1	2	5	1	6	2	1		18 (5)
16			(1)	(1)		(1)		(1)	(1)				44 (42)
				2	7	15	9	8	3				
<i>POTENTILLA</i>		2	(4)	(4)	(17)	(9)	(7)	(1)				1	1 (0)
ASPEN		13	1 (5)	1 (3)	2 (1)	10		2	1				17 (9)

*Dead white spruce has been combined with dead black spruce in Stand 16 - see totals in Table 12.

XII. THE PHYTOSOCIOLOGICAL-EDAPHIC AFFINITIES OF BLACK SPRUCE
WETLAND COMMUNITIES OF JASPER AND BANFF TO THOSE OF OTHER
AREAS IN ALBERTA AND CANADA

A. Some Past and Present Concepts of Peatland Dynamics and
Classification

One of the objectives of this thesis was to relate the peatland black spruce communities of Jasper and Banff (the *TOMENTHYPNUM* stands of this thesis) to the wooded peatland vegetation of the rest of Alberta and Canada. It soon became apparent that, in the case of Alberta, there would be some difficulties in fulfilling this objective. E. H. Moss's classification of the peatland of Alberta is now of limited usefulness, as it is based upon concepts of peatland dynamics which no longer appear valid. This does not detract from the value of Moss's information concerning the floristic aspects of northern Alberta peatland.

Much of the vegetation of North America has, in the past, been classified within a geographic-successional framework. The fundamental concepts embodied in these systems of classification are those of linear plant succession and the "climax" plant community. These concepts are discussed in Kormondy (1969; pp. 154-163) and Odum (1959, pp. 257-270). Odum presents the essential points as follows:

"Ecological succession is the orderly process of community change; it is the sequence of communities which replace one another in a given area. Typically, in an ecosystem, community development begins with pioneer stages which are replaced by a series of more mature communities until a relatively stable community is evolved which is in equilibrium with

the local conditions. The whole series of communities which develop in a given situation is called the "sere"; the relatively transitory communities are called "seral stages" or seral communities, and the final or mature community is called the "climax".

It was first postulated that there was only a single true climax for a given region - the "climatic" climax, which was the terrestrial mesophytic plant community which was self-perpetuating and in harmony with average regional climatic conditions.

According to this interpretation, which had its most ardent supporter in Frederick Clements (1916), all successional trends originating in local relatively hydric or xeric environments converged and culminated in the single climax. This conception is no longer widely accepted, though it does have practical application when the potential vegetation of very large areas is being described and mapped (as for instance, in Eyre's recent (1968) description of the vegetation and soils of the world).

It has long been realized, however, that powerful local edaphic or disturbance factors can result in the production of stable communities which bear little resemblance to the climatic climax of the region. This realization has led to the recognition of "edaphic" climaxes and "disclimaxes" respectively. The "polyclimax" approach to vegetation dynamics has become well-established in North America (see *e.g.* Oosting 1956; Daubenmire 1968; Odum 1959; Whittaker 1951, 1953; Kormondy 1969).

The concepts of linear succession and limited

convergence to climax appear to be quite valid when applied to many upland vegetations and thus have formed useful theoretical skeletons for many systems of vegetation classification.

One of the most quoted North American examples of simple linear succession and the trend from diversity to uniformity is that of the "hydrosere". In the classic hydrosere of ponds and small lakes, the "pioneer" community is an aquatic one, which gives way in time to a series of wetland communities and finally to a mesic terrestrial one. These changes in vegetation are correlated with, and a result of, the filling in of shallow bodies of water by organic matter deposited by the various plant communities. Peat mosses (*e.g.* *Sphagnum* spp.) usually play a very important role in this pond-filling sequence of northern regions.

The hydrosere model, though no doubt valid in certain instances, has had an inordinate impact on the development of North American peatland research and classification. In many areas, including Alberta (*e.g.* Moss 1953a and b) peatland communities have been described and classified almost solely according to their relative position on the assumed hydrosere of the region. As a result, the fact of the inherent complexity of peatland has been little stressed and little attention has been given to such important aspects of the peatland-vegetation complex as water chemistry. The degree of minerotrophy of a given peatland area is now recognized in North America as having a profound impact on

its floristics and successional tendencies, primarily because of the recent investigations of Fennoscandia botanists into Canadian peatlands.

In a recent paper on the peatlands of the Lake Agassiz basin in Minnesota, Heinselman (1970) advocates the Fennoscandia approach to peatland classification. He states (p. 258):

"Examination of the implication of this case history leads to the perennial question of the direction of peatland development. The term 'climax' is avoided because, as Sjörs has pointed out, it contributes little to understanding changes in northern peatlands. But even the word development, which seems unavoidable, implies direction. Much of the earlier literature concerned the basin-filling sequence (hydrarch succession) and the phytosociological evidence for development toward mesophytism.* As a result the idea of bio-automatic progression toward mesophytism with peat accumulation permeates our thinking."

Some of the more significant points brought out in this Lake Agassiz study (Heinselman 1963, 1970) are as follows: (Heinselman 1970, p. 258):

"There has been no consistent trend toward mesophytism, terrestrialization, or even uniformity. Rather, there has been a general swamping of the landscape, rise of water tables, deterioration of tree growth, and a diversification of landscape types.....If any direction is apparent it is mainly a trend toward elaboration of landscape types in the Lake Agassiz Peatlands Natural Area. Mostly the impression is one of ceaseless and almost random change, initiated by innumerable local or regional events. The plant communities and peatland types do change predictably if the full sequence is known, but what occurs in any given area depends on an extraordinarily complex series of interactions. Such a course of events

*Here he notes E. H. Moss's classification of Alberta peatland vegetation as an example, among others.

can hardly be viewed as a fixed succession."

It is probably safe to conclude that, as yet, we have only a very imperfect understanding of peatland dynamics. The studies of Heinselman in Minnesota and those of Sjörs and other Fennoscandians in northeastern Canada could well serve as models for future peatland research in this country. Quantitative data on physical and chemical environmental factors are of the utmost necessity in descriptions of peatland and should rank equally with information of a phytosociological nature.

B. The Peatlands of the Hudson Bay Lowlands

1. Ontario (Hugo Sjörs 1959, 1961, 1963)

Sjörs' papers concerning the peatland of the Hudson Bay Lowlands of Ontario have, more than any other reference, furnished me with considerable insight into the phytosociologic-edaphic relationships of the peatland of Jasper and Banff. The two areas are widely separated geographically, but nevertheless exhibit a considerable degree of floristic (and probably ecological) similarity.

The Lowlands are underlain by almost horizontal strata of Palaeozoic age. This bedrock, like that over much of Alberta, is rich in lime. The bedrock of the Lowlands rarely outcrops, however, and is overlain by calcareous clay deposits of glacial and marine origin. Postglacial isostatic uplift is still active along the coast of Hudson Bay.

The climate of the region ranges from subarctic along the coast to boreal further inland. Most of the Lowlands

lie within the discontinuous permafrost zone. The area contains over 110,000 sq. miles of peatland, much of which is treeless. The paucity of trees is believed by Sjörs to reflect edaphic rather than climatic extremes.

Both minerotrophic and ombrotrophic peatlands are present in abundance - the two types often being in very close association and reflecting, in a very sensitive fashion, local groundwater conditions. Forests, usually dominated by black spruce, are present on both peatland and mineral soil.

Sjörs emphasizes that the present distribution of peatland types is the result of very complex interactions between biota and physical environment. However, his generalized description of peatland development in the Lowlands is as follows. After the retreat of marine waters, the uplifted clay sediments were occupied by rich forest. The forest vegetation and its organic deposits probably led to poorer drainage and wetter conditions (paludification) over much of this very level landscape. Sjörs suggests that the dam-building activity of beaver may also have been a prime factor in bringing about the initial stages of the paludification process. The swamp forest, with increasing wetness, developed into wooded fen, which then evolved into open fen or ombrotrophic bog. Bogs may also have developed directly from forest on mineral soil, without the fen stage.

It is significant that areas nearest the coast of Hudson Bay, having been uplifted relatively recently, support much more fen, and relatively less bog, than areas further inland.

The bogs of the Hudson Bay Lowlands have great floristic affinity to those of Fennoscandia. Sjörs lists 34 vascular species found in definitely ombrotrophic bogs in the Attawapiskat River area of the Lowlands, compared to only 24 for the bogs of entire Fennoscandia, reflecting the greater richness of the North American flora. Further, no less than 15 vascular species are shared by the bogs on both sides of the Atlantic, and their habitat relations appear identical in both areas. The bryophyte flora is even more similar.

Of the 34 vascular species listed for bogs in the Hudson Bay Lowlands, 29 are known to be present in Alberta peatlands. Many could probably be used as indicators of bog conditions here. The species shared are:

Picea mariana
Larix laricina
Andromeda polifolia
Carex limosa
C. oligosperma
C. paupercula
C. pauciflora
C. trisperma
Chamaedaphne calyculata
Gaultheria hispidula
Drosera rotundifolia
D. anglica var. *pusilla*
Empetrum nigrum
Eriophorum chamissonis (*E. russeolum*)
E. vaginatum
Geocaulon lividum
Kalmia polifolia
Ledum groenlandicum
Nuphar variegatum
Rubus chamaemorus
Sarracenia purpurea (rare in Alberta)
Scheuchzeria palustris
Scirpus caespitosus
Smilacina trifolia
Oxycoccus microcarpus
Oxycoccus quadripetalus
Vaccinium myrtilloides
V. uliginosum
V. vitis-idaea

It should be noted that not all of these species are restricted to bog habitats - but they can all tolerate such edaphic extremes.

Only 6 of the above "bog species" occur in one or more of the sampled black spruce communities of Jasper and Banff. Besides black spruce, these are *Ledum groenlandicum*, *Empetrum nigrum*, *Geocaulon lividum*, *Oxycoccus microcarpus* and *Vaccinium vitis-idaea*.

The rich fen and rich forest flora of the Lowlands, in contrast, is much more similar to that of my black spruce communities. The extremely rich fens grade into black spruce forests which have developed on moist mineral soil without much peat accumulation. Sjörs (1961, pp. 8-10) includes a Presence list compiled from 5 rich, relatively open black spruce forests near Hawley Lake. The influence of the lime-rich substrate is evident. A total of 54 subordinate vascular species are listed, no less than 32 of which are present in at least one of the Jasper-Banff stands, many being well represented by frequency and cover data.

The 32 species shared are:

Betula galandulosa
Arctostaphylos rubra
Geocaulon lividum
Juniperus communis
J. horizontalis
Ledum groenlandicum
Linnaea borealis
Potentilla fruticosa
Rosa acicularis
Salix myrtillofolia
S. vestita
Shepherdia canadensis
Vaccinium caespitosum
V. vitis-idaea

Anemone parviflora
Aster ciliolatus
Castilleja septentrionalis
Cornus canadensis
Fragaria virginiana
Mitella nuda
Petasites palmatus
Rubus acaulis
Senecio pauperculus
Solidago multiradiata
Viola adunca
Agropyron trachycaulon
Calamagrostis canadensis
Carex concinna
C. scirpoidea
C. vaginata
Elymus innovatus
Equisetum scirpoides

It is important to note that Sjörs' species list is from black spruce "forests" developed on mineral soil - not from wooded peatland. Some of his 5 stands seem to bear more resemblance to my *POTENTILLA* stands than they do to the majority of *TOMENTHYPNUM* stands. Most of my *TOMENTHYPNUM* stands would be more analogous to Sjörs "fen" communities on account of their peaty substrate and presence of standing water in many of the hollows. Sjörs' open and wooded "extremely rich" fens contain most of the above species as well as some others which prefer wetter or more exposed substrates. Some of these additional fen species which also occur in my Jasper-Banff stands are *Parnassia palustris*, *Pinguicula vulgaris*, *Pedicularis groenlandica*, *Polygonum viviparum*, *Tofieldia glutinosa*, *T. pusilla*, *Carex aquatilis*, *C. capillaris*, *C. gynocrates*, *C. leptalea*, *Equisetum variegatum*, *Eriophorum brachyantherum* and *Triglochin maritimum*.

It is evident that there is a remarkable affinity

between the vascular flora of the lime-rich wetlands of the two widely separated areas. Sjörs discusses the micro-habitat relations of many of the rich fen species. The same species appear to have very similar ecological amplitudes in Alberta, suggesting that much of Sjörs phytosociological information can be directly applied to Alberta peatland.

The bryophyte strata of the extremely rich fens of the Lowlands also appear to be floristically similar to those of Jasper-Banff *Tomenthypnum* communities. Shared dominants in both areas are *Tomenthypnum nitens*, *Aulacomnium palustre* and *Sphagnum warnstorffianum*. Other shared species are *Campylium stellatum*, *Drepanocladus revolvens* and *Calliergon giganteum*. All of the above species are reliable indicators of minerotrophic conditions. Two common mosses of the Lowlands extremely rich fen which were not found in my Jasper-Banff communities are *Scorpidium scorpidioides* and *Drepanocladus intermedius*.

Sjörs (1961, p. 5 and 15) presents some water chemistry data related to extremely rich fen vegetation near Hawley Lake in the Lowlands. The pH ranges from about 7.1 to 8.3. Calcium and magnesium ions from Hawley Lake water are 32 and 7 ppm respectively. These concentrations are certainly high, but the Jasper-Banff concentrations of calcium and magnesium are even higher (see Table 4, p. 61).

In conclusion, there can be little doubt that the sampled Jasper-Banff black spruce peatland forests would fall in the "extremely rich fen" category of the

Fennoscandian peatland terminology framework. The fens of Jasper and Banff have a great many species in common with those of the distant Hudson Bay Lowlands.

2. Manitoba (Ritchie, 1960)

Ritchie describes "larch fens" and "shrub fens" from the more northern portion of the Lowlands, which lies in Manitoba. He is in essential agreement with Sjörs in postulating that a natural succession from marsh to fen to bog is prevalent in the Lowlands and parallels the "aging" of sites following emergence from Hudson Bay.

The fens of northern Manitoba occupy wet shallow (<1m) peats overlying calcareous clay. Ritchie's phytosociological data are not detailed enough to allow rigorous comparison but it is evident that the moss layers of the fens of northern Manitoba and those of Jasper and Banff are similar in species composition and identity of dominants. *Sphagnum warnstorffianum* and *Tomenthypnum nitens* (associated with *Aulacomnium palustre*) are the usual peat-forming mosses in the fens of these widely-separated areas. *Drepanocladus revolvens*, *D. uncinatus* and *Calliergon giganteum* are abundant in the wettest portions of the northern Manitoba fens - they occupy a similar niche in my *TOMENTHYPNUM* stands. The vascular strata show less floristic affinity, however. Many of the species listed by Ritchie were not found in my Jasper-Banff stands, but are known to be present in Alberta peatlands. Two examples are *Smilacina trifolia* and *Rubus chamaemorus*. Their abundance in Ritchie's fens probably

reflects the abundance of *Sphagnum* relative to the more alkaline substrate provided by *Tomenthypnum*.

The dominant shrubs in Ritchie's fens are *Betula glandulosa* and *Salix pedicellaris* var. *hypoglauca*. *Ledum groenlandicum*, a dominant in my *TOMENTHYPNUM* stands, is apparently scarce in the fens of northern Manitoba. Also, black spruce is evidently not abundant in the minerotrophic peatland of northern Manitoba, but is supplanted by sparse, depauperate tamarack.

C. The Peatland of Northern and Northwestern Alberta

1. The System of Classification Proposed by Moss

(1953 a & b; 1955).

The late E. H. Moss recognized 3 wooded wetland associations. The "black spruce - peat moss" association is generally characterized by a *Sphagnum*-dominated moss stratum and is held to have arisen in depressions through acid bog stages with the production of considerable peat. This community is interpreted by Moss as being subclimax, although it can be maintained by fire and/or frequent flooding. Moss postulates a natural succession to a "black spruce - feather-moss" association.

The "black spruce - feathermoss" association is interpreted as either having developed on level terrain without much peat accumulation, or alternatively, can develop as the end-point (edaphic climax) of the bog succession sequence. This association apparently has considerable phytosociological affinity to the upland boreal spruce-fir climax

community.

Moss's "tamarack (*Larix laricina*) association "has some features in common with the "black spruce - peat moss association" but differs in its development, *i.e.* from a "Drepanocladus - Carex - Betula bog" under persisting wet conditions.

Moss linked these various communities in the dynamic (hydrosere) sequence shown in Figure 8 . The seral tendencies have been extracted from Moss (1955, p. 529-534).

A number of points in connection with the model deserve attention:

1) Although earlier papers on Alberta peatland (Lewis and Dowding 1926; Lewis, Dowding and Moss 1928) included data on the physical environment, including water chemistry, Moss does not provide any such data in subsequent papers. Some rather sporadic information on peat depths and types of peat are presented in the discussion of specific bogs (Moss 1953b). Qualitative comments on the wetness or dryness of the site and the possible influences of fire and flooding in the past are given some attention, but, on the whole, information is primarily of a taxonomic-phytosociological nature.

2) The term "bog" is variously used by Moss. In one paper (Moss 1953b, p. 450) he defines the term as follows:

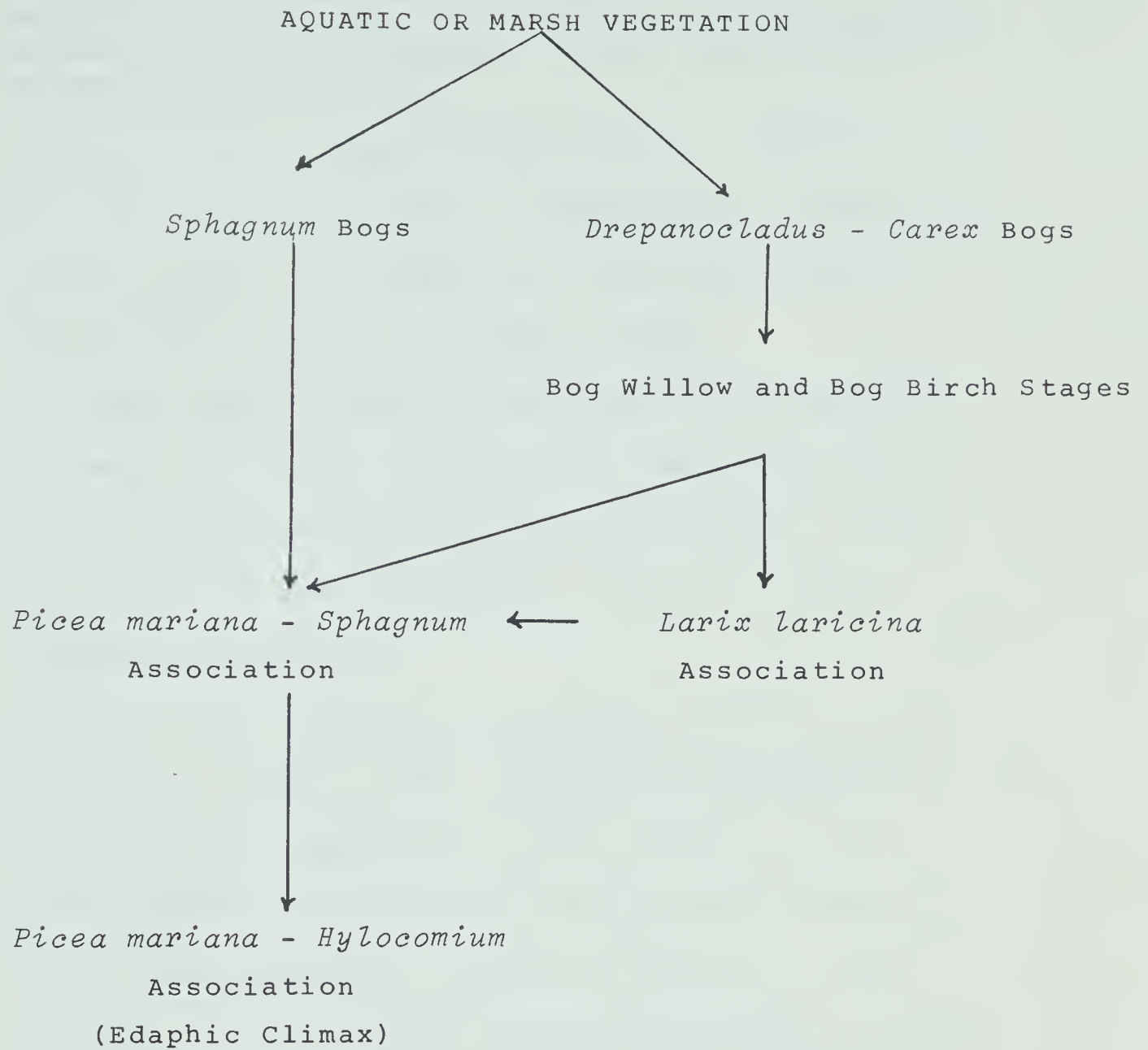


FIGURE 8. E. H. Moss's Hydrarch Succession Model for Northern Alberta Peatland.

"A bog is characterized by conifers (notably *Picea mariana* in our region), by ericads, by peat-forming mosses, commonly *Sphagnum*, and by a cushionlike substratum of raw peat."

He also implies considerable acidity. However, in his 1955 paper (p. 557) he mentions the "unique calcareous bogs" near Edmonton, which were earlier described by Lewis and Dowding (1926).

Moss does not employ the word "fen" and omits any mention of the influence of lime-rich groundwater on peatland floristics and dynamics, except for his brief acknowledgement of the calcareous bogs mentioned above.

3) The "type" floristic description given by Moss (1953a, p. 221) for the "*Sphagnum* bog" indicates that the most common flowering plants are *Ledum groenlandicum*, *Vaccinium vitis-idaea* var. *minus*, *Rubus chamaemorus* and *Smilacina trifolia*. Less constant species include *Betula glandulosa*, *Vaccinium oxycoccus*, *Equisetum sylvaticum*, *Eriophorum spissum* and various species of *Carex*. An uneven carpet of *Sphagnum*, mainly *S. fuscum* and *S. capillaceum*, is present and *Cladonia* lichens are common.

I believe that this is a valid description of the highly acidic cation-poor peatland of northern Alberta - roughly analogous to the "poor fens" and "ombrotrophic bogs" of Sjörs (1959, 1961, 1963). It is apparent that these communities have little

in common with my Jasper-Banff *Tomenthypnum* stands, although they may be wooded with black spruce (the "black spruce - peat moss association" of Moss) and contain abundant *Ledum groenlandicum*. It is obvious that both of these species have a broad ecological amplitude in regards to soil reaction.

4) Moss's "*Drepanocladus* - *Carex* bogs", by contrast, give considerable evidence of minerotrophy and could more appropriately be termed "*Drepanocladus* - *Carex* fens". These wet communities are rich in species, many of which are known calciphytes. Moss postulates that this community is intermediate between early aquatic and marsh stages and later *Sphagnum* bog stages in the assumed hydrosere of the region.

5) Moss's "*Larix laricina*" wetland association is very definitely a fen complex and has a great deal of floristic affinity to black spruce wooded fen communities of Jasper and Banff - with the obvious qualification that tamarack is present in none of my stands!

It is, therefore, particularly unfortunate that Moss devoted relatively little attention to this association and that no chemical data are presented for it. The description of the association, though brief, includes a list of typical species (Moss 1953a, p. 225-226). Twenty-five of the 60 vascular species listed are present in my *TOMENTHYPNUM* stands and

many of them are very frequent components of the shrub and herb layers - e.g. *Betula glandulosa*, *Carex aquatilis*, *C. gynocrates*, *C. leptalea*, *C. capillaris*, *C. vaginata*, *Arctostaphylos rubra*, *Rubus acaulis*, *Habenaria obtusata* and *Pyrola asarifolia*.

Among the dominant mosses listed are *Tomenthypnum nitens* and *Aulacomnium palustre*.

Moss's "tamarack association" contains black spruce as well as tamarack. He postulated that the tamarack community proceeds naturally to the "black spruce - *Sphagnum* association" and that the tamarack association itself develops from the "*Drepanocladus* - *Carex* bog". This generalized development sequence, explained by Moss in terms of the hydrosere, should not be discounted, as it appears to parallel the trend from calcareous marsh to fen to bog described by Sjörs (1959, 1961, 1963), Ritchie (1960) and Heinselman (1963, 1970). Whether or not this trend is universal is open to question. It is known that it can be quickly reversed by fire or flooding with calcium-rich groundwater.

It nonetheless appears that Moss's proposed successional sequences, explained totally on the basis of progression towards mesophytism from a hydric state, are possible in many sites but that a parallel trend from minerotrophic to ombrotrophic

condition must be appreciated in order to understand the floristic changes which occur.

Whether or not this generalized trend terminates in a "black spruce - feathermoss" forest (the peatland edaphic climax of Moss) is seriously open to question, however, as is the suggestion that the sequence applies to most of Alberta peatland.

Paludification - the direct entry of peat mosses to moist, but not aquatic, sites and the consequent rise in water tables is probably more common than the basin-filling sequence which forms the basis of Moss's framework. Studies of the paludification process (*e.g.* Heinselman 1970) suggest that there is no general trend towards closed feathermoss forest from the bog condition. In fact, the opposite may well occur and surrounding forested uplands may be converted to open peatland.

2. Lewis and Dowding (1926) - Peatland near Edmonton

Lewis and Dowding described the marshes and muskegs within a 30 mile radius of Edmonton. They give chemical data as well as floristic information. Some of their findings may be relevant to the peatlands of Jasper and Banff.

One of their more significant observations deals with a case of retrogression from *Sphagnum* - black spruce peatland to rich wet fen due to flooding of the former with lime-rich groundwater. Their observations indicate that a small glacio-lacustrine basin near Edmonton was at one time totally

occupied by wooded *Sphagnum* peatland. Subterranean springs of lime-rich water subsequently broke into this peatland, causing the destruction of much of it and replacement by rich marsh and wet fen (the "*Scirpus* bogs" and "*Carex* bogs" of Lewis and Dowding) and lake. Their water chemistry data indicate that this aspect of the physical environment is not very different from that of Jasper-Banff peatlands. The pH of the water in the remaining *Sphagnum* peatland is 4.5, while that of water within the "*Carex* bog" was 7.5. The lake water had a pH of 9. Calcium and magnesium concentrations in the water of the lake and floating vegetation were very high - from 53 to 86 ppm calcium and from 26 to 41 ppm magnesium. These values are similar to those obtained from Jasper and Banff (see Table 4 , p.61).

Coinciding with the change from acidic peatland to fen and marsh is a change from *Sphagnum* mosses to a group of mosses Lewis and Dowding referred to as "*Hypnum*". I believe that this "*Hypnum*" complex probably includes *Tomenthypnum nitens* and possibly various species of calcicolous *Drepanocladus* as well. I base this assumption on personal observations made in the same district. Small, highly localized discharges of lime-rich groundwater are not uncommon within the *Sphagnum* - black spruce peatlands near Edmonton (north of Winterburn, especially). There is usually an abrupt change from the *Sphagnum* (species not determined) to *Tomenthypnum nitens* at such sites. In the warmest periods of the summer, this latter moss may even be encrusted with

carbonate.

3. The Peatland of the Foothills of West-Central Alberta
(Hinton-Edson District) - Horton and Lees (1961).

The Horton and Lees study of the black spruce and its habitat in the Alberta foothills was concerned primarily with the commercial productivity of this species in relation to site conditions, although some synecological information is also presented in the discussion of habitat.

Horton and Lees use moisture regimes to delimit site classes and it is possible to relate many of my stands to their moisture spectrum. Moisture regime 9 is referred to as "marsh". Moisture regimes 8 and 7 are termed "deep bog" and "shallow bog" respectively. All of my *TOMENTHYPNUM* stands would probably fall in these categories. Moisture regime 6, termed "bog border" would include Stands 1 and 16 of my *HYLOCOMIUM* Group. Stands 11 and 13 of this Group would fall in moisture regimes 2 and 3, referred to as "mesic upland". The Mixed Character stands of this thesis would occupy Horton and Lees moisture categories 6, 7 and 8.

Chemical data is scant but the authors note that calcium-rich peatland is abundant in the foothills. No "truly acid" bogs were found, according to the authors, and soil pH ranged from 5.5 to 8. It is apparent then that the term "bog" is synonymous to "peatland" in Horton and Lees' paper, and does not imply highly acidic oligotrophic conditions.

Enough phytosociological data is presented to permit

a rough comparison between peatlands of the foothills and that of similar moisture regimes in Jasper and Banff.

The "marsh" community of Horton and Lees, which supported few scattered black spruce and tamarack, appear to be botanically similar to the wet species-rich sedge communities which fringe shallow calcareous lakes in Jasper. Although I did not carry out intensive studies of these communities, I did briefly visit a number of them and take some notes on species composition.

The "marshes" of the Foothills and those of Jasper and Banff are species-rich and fall in the "rich wet fen" category of Fennoscandian terminology. Both seem roughly analogous to Moss's "*Carex - Drepanocladus* bog". Horton and Lees list the most constant species as *Tomenthypnum nitens*, *Drepanocladus* spp., *Aulacomnium palustre*, *Sphagnum* spp., *Menyanthes trifoliata*, *Carex aquatilis*, *Carex leptalea*, *Juncus* spp. and *Betula glandulosa*. In Jasper, *Carex rostrata* and *C. buxbaumii* are also frequent, and commonly abundant, components of these communities.

The "deep bog" and "shallow bog" communities of the foothills typically contain the following species - *Ledum groenlandicum*, *Betula glandulosa* (the dominant shrubs in moisture regimes 7 and 8 respectively), *Vaccinium vitis-idaea*, *Salix candida*, *S. pedicellaris*, *Carex aquatilis*, *Smilacina trifolia*, *Hylocomium splendens*, *Pleurozium schreberi*, *Sphagnum* spp., *Tomenthypnum nitens*, *Aulacomnium palustre* and *Drepanocladus* spp. The dominant mosses of the "wetter"

(deep bog) stands are *Sphagnum* and *Tomenthypnum nitens*.

The drier bogs, while retaining *Sphagnum* as a dominant, also contain the mosses *Hylocomium* and *Pleurozium* in abundance.

Detailed floristic comparisons between my stands and those of Horton and Lees are probably dangerous. Much of their information consists of Constance data only, which is of limited value. No information is provided on the distribution of herb and shrub species relative to hummocks and hollows and the nature of the moss substrate. Nevertheless, it does appear that the Jasper-Banff wetland black spruce communities have considerable phytosociological affinity to those of the foothills. Of the 70 subordinate species listed by Horton and Lees, 48 appear in one or more of my stands. It also appears that, although the foothills peatland is more or less minerotrophic, *Sphagnum* is more abundant than in the adjacent mountain parks.

4. Summary - The Peatlands of Northern Alberta

It is apparent that we as yet know relatively little about the peatlands of central and northern Alberta. The work of E. H. Moss, should not be considered definitive - it is only (as Moss himself emphasized) a first step. Moss's most valuable contribution was in the field of the floristic aspects of wetland communities. We now know which species can be found in such habitats. However, perhaps because he was over-influenced by hydrarch succession concepts, Moss almost totally ignored the reciprocal effects of water chemistry and peatland vegetation.

The fact that much of the parent soil material of Alberta (glacial drift, glacio-lacustrine deposits, aeolian deposits) is derived from lime-rich bedrock (predominantly Cretaceous) suggests that minerotrophic peatland is not at all uncommon. In fact, it is possible that Alberta, especially western Alberta, contains some of the most lime-rich peatland in North America. This possibility, apparently not recognized by Moss, must be taken into account if we are to understand the vegetation and dynamics of Alberta peatlands. We must also, as Heinselman (1970) suggests, employ the "climax" concept with caution in regards to peatland, at least until we have more solid evidence for it.

Below are some tentative conclusions regarding the relationship of Jasper and Banff peatlands to those of central and northern Alberta:

a) Moss's "*Drepanocladus* - *Carex*" bog, Lewis and Dowding's "*Carex* bog" and Horton and Lees' "marsh" are probably all wet, rich fen communities which develop in shallow water rich in bicarbonates of calcium and magnesium. All of these communities appear to have close phytosociological affinity to the wet lowland sedge communities of Jasper. These communities may appear as floating mat or may occupy a more consolidated substrate. They are probably maintained in this stage by frequent flooding. In the absence of flooding they may progress to a less minerotrophic type of peatland, associated with the invasion of *Sphagnum*. Typical species of this rich fen community over much of northern

Alberta are probably *Betula glandulosa*, *Carex aquatilis*, *Carex leptalea*, *Carex rostrata*, *Menyanthes trifoliata*, *Drepanocladus* spp., *Aulacomnium palustre* and *Tomenthypnum nitens*. It is important to note, however, that this community can be very rich in species due to considerable habitat diversity. A strong representation of calciphytes is probably typical. Scattered tamarack and black spruce, usually exhibiting very stunted growth, are not uncommon in these communities, even in the "floating sedge mat" phase.

b) Moss's "tamarack association" is probably a dryer, wooded, variant of the above rich fen community. The substrate is probably more consolidated. This association definitely exhibits rich fen characteristics and has a great deal of phytosociological affinity to my "*Tomenthypnum*" communities. It would probably also include some of Horton and Lees' dryer marsh and their "deep bog" communities. Though tamarack is usually the dominant tree, black spruce is also common and totally replaces the tamarack in Jasper and northern Banff. Typical species of this rich, moist to wet wooded fen are probably *Betula glandulosa*, *Ledum groenlandicum*, *Salix* spp., *Arctostaphylos rubra*, *Rubus acaulis*, *Vaccinium vitis-idaea*, *Vaccinium oxycoccus* (= *Oxycoccus microcarpus*), *Petasites* spp., *Pedicularis* spp., *Habenaria obtusata*, *Senecio pauperculus*, *Pyrola asarifolia*, *Equisetum* spp., *Carex disperma*, *C. lasiocarpa*, *C. rostrata*, *C. aquatilis*, *C. gynocrates*, *C. leptalea*, *C. capillaris*, *C. vaginata*, *C. paupercula* and *Calamagrostis inexpansa*. An abundance of

mosses *Tomenthypnum nitens* and *Aulacomnium palustre*, both good indicators of a lime-rich substrate, is typical. In the wettest parts of the community mosaic *Drepanocladus* spp. are usually abundant. A number of species of *Sphagnum* are usually also present and they may help to introduce the acidophytes such as *Rubus chamaemorus* and *Smilacina trifolia*. *Sphagnum*, however, does not totally dominate the moss stratum of this floristically diverse community.

It is important to note that the above description applies to the richest type of wooded fen (the trees not producing a complete "canopy" of foliage. Every gradation exists between this "type" and the "true bog" vegetation. There is considerable evidence to suggest that, barring periodic flooding by lime-rich water or severe peat fires, this community does tend to become invaded by *Sphagnum* and to become less minerotrophic and, as a result, less rich floristically. Periodic floods of lime-rich water or severe fire probably act to reverse this tendency and maintain rich fen woodland.

c) Moss's "*Sphagnum* bog" and "*Picea mariana* - *Sphagnum* Association" in general represent a much more extreme type of peatland - poor fen and ombrotrophic ("true") bog. The number of vascular species is much lower and the dominants are usually *Sphagnum* spp. (*S. fuscum* and *S. capillaceum* being especially noted by Moss). *Ledum groenlandicum* is the dominant shrub and its presence in abundance may prevent shade-intolerant tamarack seedlings from becoming

established. In the types of bog in which trees are abundant, black spruce is the normal dominant. *Vaccinium vitis-idaea*, *Rubus chamaemorus*, and *Smilacina trifolia* are generally abundant and *Cladonia* lichens commonly occupy the tops of the drier *Sphagnum* mounds. The water held by the *Sphagnum* is highly acid and low in dissolved calcium. The above generalizations are based on limited observations of such vegetation in northern Alberta and the "type" description given by Moss. Other ericaceous species, such as *Chamaedaphne calyculata*, *Andromeda polifolia* and *Kalmia polifolia* are frequently present in northern Alberta bogs.

This type of peatland is apparently not common in the Foothills of western Alberta, or within Jasper and Banff Parks. It is abundant, however, in the northern half of Alberta, east of the Foothills.

This type of peatland can probably develop in at least two ways in northern Alberta, as suggested by Moss. Very often, peat samples (see Hansen 1952; Lewis and Dowding 1926) suggest that the *Sphagnum* has directly invaded a moist, but not necessarily wet, water-covered heavy mineral soil. The growth of *Sphagnum*, by acting as a "sponge" would result in general paludification of the site, blocking drainage. The *Sphagnum* substrate would tend to grow vertically as well as laterally and would raise its associated moisture regime with it. The result of such a development is the classic "ombrotrophic" convex bog of Sjörs and Heinselman, in which virtually all nutrients are supplied by rain and dust fallout.

This sequence would be expected in areas in which groundwater is not rich in bicarbonates (*e.g.* Canadian Shield) or in those in which water tables remain relatively constant for long periods of time, as in the broad, flat, glacio-lacustrine deposits of silt and clay in northwestern and central Alberta (*e.g.* Peace River - Grande Prairie district; Glacial Lake Edmonton district).

Another way in which poor fen or ombrotrophic bog can develop is by replacing a rich or moderately rich fen (as represented by Moss's tamarack association). As I have already emphasized, this is probably not a tendency of all such rich peatland, but would be expected, once again, in those parts of Alberta in which water tables do not rise and fall by large amounts. The tendency would thus be greatest in areas removed from the mountains and foothills.

In fact, I strongly suspect that the reason why this type of peatland decreases in abundance as the mountains are approached is two-fold. First, calcium rich bedrock comes closer to the ground surface as the mountains are approached. The Front Range of the Rockies contain large amounts of limestone and calcareous shale. Secondly, water tables rise and fall rapidly as the heads of the Alberta watersheds are approached. Such conditions would tend to maintain highly minerotrophic peatland by discouraging the complete take-over of *Sphagnum*. This hypothesis should be investigated thoroughly, possibly by experimental control of a number of small mountain watersheds.

It is probably doubtful if all *Sphagnum* peatland will develop in time into a black spruce - feathermoss closed forest, as Moss suggests. There are known cases of this, and such a trend is certainly possible, though not universal. Paludification of uplands by *Sphagnum* and rising water levels over large areas are probably at least as common phenomena (Heilman 1966; Heinselman 1963).

XIII. DISCUSSION OF THE SUCCESSIONAL TENDENCIES OF BLACK
SPRUCE COMMUNITIES IN JASPER AND BANFF.

A. Upland Black Spruce

The term "upland" as used here implies an usually well-drained, level or sloping site, irrespective of altitude, in which the water table has no effect on the surface soil moisture regime. Only two stands (11 and 13) would fit this description.

Excluding the small areas of poplar forest in Jasper and Banff, there are essentially two major types of sub-alpine forest in the parks - the climax spruce-fir forest and the lodgepole pine forest, the latter usually traceable to past fires (Hnatiuk 1969). Black spruce is a frequent but generally not abundant component of the climax spruce-fir forest, which is usually dominated by white spruce, and/or Engelmann spruce and alpine fir (Beil 1966). It is also frequently found in the understory of lodgepole pine forests but usually attains abundance only where the pine forest abuts a body of black spruce peatland. Relatively pure upland black spruce stands can be expected to emerge on many of these sites but they will occupy relatively little area relative to the typical spruce-fir forests. These future upland black spruce forests will no doubt be eventually invaded by subalpine fir and will then form a variant of the spruce-fir climax in which black spruce is more abundant than usual.

The relative abundance of black spruce in the upland

spruce-fir climax seems to be largely a function of three factors - local edaphic conditions, proximity of peatland and, perhaps most importantly, the frequency of fires preceding a long fire-free period. Frequent intense upland fires, while promoting pine, place black spruce on the same initial competitive footing as white spruce, Engelmann spruce and alpine fir. It is important to recognize that upland black spruce is a "fire species" only if a large component of its population is bearing cones at the time of the fire, and frequent upland fires make this impossible. Slow recolonization of uplands from "refugia" must then take place after each fire and, as black spruce has no initial advantage over the other shade-tolerant upland species, and may be somewhat less aggressive than these species on upland soils, it is not likely to be prominent on the uplands.

A sequence of events which would probably increase the prominence of black spruce in the uplands of Jasper and northern Banff would be a long fire-free period, allowing upland black spruce seed stocks to become well-established, followed by intense fire in the spring of the year, by which time the seed of competitive shade-tolerant species would be on the ground.

B. Wetland Black Spruce

The term "wetland" here is used to indicate those sites in which the water table is near enough to the ground surface to affect the surface soil moisture regime. Fourteen black spruce stands fall in this category, including members of

all 4 Groups. Though these stands are all characterized by a high water table, some may be quite dissimilar otherwise. In short, the "wetland" black spruce communities contain a great deal of floristic, structural and edaphic variability.

1. Peatland Succession

Only the 6 stands of the *TOMENTHYPNUM* Group can properly be termed wooded "peatland" communities in that they have a surficial organic horizon laid down by peat-forming mosses (*e.g. Tomenthypnum nitens, Sphagnum spp.*) and the water table is very close to the ground surface. These peatland communities are very similar vegetationally but seem to have developed in at least three different ways:

a) Peatland development bordering small calcareous lakes (*e.g.* base of Athabasca River Valley)

The narrow (usually only a meter or so wide) sluggish influent and affluent streams of the small marly lakes and ponds in the Athabasca River valley are often bordered by a species-rich, very wet *Carex - Drepanocladus* fen community, which is commonly floating near its border with the open water of the lake. The dominant sedges are usually *C. rostrata*, *C. aquatilis* and *C. buxbaumii*. *Betula glandulosa*, *Salix* spp. and *Potentilla fruticosa* are frequent shrubs, and the herb *Menyanthes trifoliata* is usually prominent. Stunted black spruce may be present on these sedge mats but except for seedlings, the species is rarely very abundant.

As the floating or leading edge of the sedge mat progresses out into the lake, the shoreward part becomes more consolidated and amenable to the establishment of a black

spruce-peat moss community. Consolidation probably occurs somewhat differently around the influent and effluent streams. As the influent stream meets the trailing edge of the sedge mat, its velocity would decrease rapidly, causing it to drop its suspended silt. As a result, a silt "fan" or "mini-delta" would develop immediately to the rear of the sedge mat, providing a wet, more or less mineral substrate onto which calciphytic peat mosses and black spruce could advance.

Consolidation at the effluent would probably be different in that a silt sediment would not be deposited (except during floods) and thus formation of a consolidated substrate would have to rely largely on the build-up of organic matter derived from the sedge community (as in the typical pond-filling sequence of the Canadian Shield, where there is little silt in the streams).

I would like to make clear that the above is only a tentative hypothesis, based on limited observations of these sedge mat communities. However, it is clear that siltation is a major factor in the pond-filling sequence in Alberta, in contrast to areas in the Canadian Shield, in which the bulk of the so-called "hydrosere" studies have taken place.

b) Peatland development in stream channels

Most of the small streams linking the ponds, lakes and rivers of the Athabasca River valley occupy channels which are much wider than the present stream. The fairly level gravel beds of these stream channels are usually covered with

fine-textured mineral sediments which have either been laid down during the meanderings of the present stream, or owe their existence to sheet erosion from surrounding uplands following fire, or perhaps to the past dam-building activities of beaver. Development of peatland in these channels usually proceeds without an initial aquatic stage - calciphytic peat mosses developing directly on the wet mineral substrate. Some peat deposits laid down in these channels exhibit alternating layers of peat and silt, each layer usually only a few cm thick, possibly indicating that the peat begins development in dry years.

c) Development of "Hangmoor" peatland

This type of peatland development is common in the middle altitudes of the subalpine zone. It usually occurs on concave, level, or gently sloping areas beneath ground water seepages. Peat formation by mosses probably proceeds directly without an initial aquatic stage. The peat moss, once established, acts as a blotter, absorbing much water and thereby raising the water table, and then proceeds to invade surrounding uplands.

It appears probable that much of the peatland of Jasper and Banff has developed in this manner, without an initial aquatic community. Detailed studies of peat cores are necessary before this hypothesis can be proven.

Most of the peatland of Jasper and Banff is decidedly minerotrophic and supports a rich to extremely rich fen vegetation. Studies elsewhere indicate that minerotrophic

peatland commonly progresses towards oligotrophy, with the vegetation evolving from a species-rich type to a species-poor bog community. If this trend occurs in Jasper, it is probably precipitated by establishment of the calciphytic but acid-producing *Sphagnum warnstorffianum* on wetland sites. The factors which allow *Sphagnum* to out-compete *Tomenthypnum* on calcareous substrates are therefore critical to our understanding of the fen-bog transformation. It is possible that the *Sphagnum* may not be able to tolerate extremely high concentrations of lime. If this is in fact the case, then periodic flooding of mountain peatland would tend to maintain *Tomenthypnum* and discourage *Sphagnum*. Also, rich fens would tend to be more abundant in the lowlands of the Parks, where water levels fluctuate considerably, than at higher altitudes. True *Sphagnum* bogs, if they occur in the parks, would be expected in areas where water levels do not fluctuate greatly. This hypothesis can only be tested by more field studies.

2. Frost-heaved Mineral Substrates

The fine-textured water-deposited sediments referred to in the above discussion of peatland may, under certain conditions, undergo vigorous frost-heaving, as in the vicinity of the Snaring River campground. The factors that permit frost-heaving in one location, while immediately adjacent locations are developing normally into peatland (*e.g.* Stands 5 and 6) are difficult to recognize. It is possible that the absence of trees, for whatever reason,

may be a contributory factor. It is evident that frost-heaving not only discourages the establishment of black spruce, but also that of peat mosses. Frost-heaving in wetland mineral soil can raise mineral hummocks well above the water table, providing a mineral substrate suitable for the establishment of white spruce, which has difficulty in establishing on peat mosses. Much of the frost-heaved wetland of Jasper is occupied by this species rather than black spruce (*e.g.* in Snaring River campground area). Future development of these frost-heaved sites is difficult to predict, but peat formation may begin in the damp hollow and then eventually spread to the hummocks, or an areal equilibrium state between peat and mineral substrates may exist.

3. Closed Canopy Wetland Forest (Lodgepole pine in overstory)

This type of wetland forest (best represented by Stands 1 and 16 of the *HYLOCOMIUM* Group) differs from the peatland forest (*TOMENTHYPNUM* Group) in having an overstory of pine. The presence of pine appears to discourage the growth of peat-forming mosses such as *Tomenthypnum* and *Sphagnum*, both of which prefer medium to high light intensities. The pine creates shade both directly and indirectly. Black spruce developing beneath wetland pine grows rapidly and tall. This black spruce foliage fills the spaces between and below the pine canopy, producing a very shady forest interior. Such conditions promote the growth of *Hylacomium* and other feathermosses on wetland sites.

This type of wetland community can remain as a "feather-

moss wetland forest" if the shade can be maintained. Once the pine has reached senescence and begins to fall, its place must be taken by additional spruce or, more effectively perhaps, by alpine fir.

If, however, the forest "breaks up", allowing light penetration to the ground, then eventual takeover by peat mosses would probably occur in many cases and progression towards a wooded peatland community, with very different physiognomy and floristics, would take place.

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APPENDIX A

INDICES OF DISSIMILARITY BETWEEN STANDS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1															
2	85.8														
3	60.1	85.8													
4	63.9	93.3	32.0												
5	68.9	94.5	56.8	51.6											
6	81.2	66.6	79.9	85.3	85.5										
7	50.7	85.5	52.5	55.8	62.3	76.0									
8	69.4	92.2	42.9	40.8	40.9	86.2	49.2								
9	74.3	95.3	58.5	43.1	48.8	91.4	60.1	56.3							
10	79.3	96.8	42.0	44.5	44.3	90.3	50.0	37.3	58.4						
11	56.9	80.5	61.1	72.7	76.6	68.8	62.4	79.2	83.9	80.4					
12	81.9	95.1	57.4	58.9	46.9	86.8	77.2	66.8	63.1	45.6	70.0				
13	45.0	85.1	72.3	78.2	84.5	81.8	70.7	81.8	88.1	87.8	45.7	83.2			
14	85.0	94.9	58.9	56.4	36.4	86.0	79.4	59.0	59.5	42.4	72.5	24.9	85.8		
15	54.1	89.6	53.3	43.1	64.3	91.6	46.9	55.8	42.4	69.5	80.9	79.3	72.3	74.4	
16	74.0	98.2	86.8	72.4	91.7	96.3	88.1	90.4	84.4	81.5	80.2	78.8	66.7	89.1	87.3

APPENDIX B.1. Procedure followed in Construction of 2-Dimensional
Stand Ordination (after Orloci (1966)).

Terms Used in Equations:

R_1 = first end stand of X-axis
 R_2 = second end stand of X-axis
 R_3 = end stand of Y-axis
 D_{12} = dissimilarity between R_1 and R_2
 = length of X-axis
 D_{1j} = dissimilarity between stand j and stand R_1
 D_{2j} = dissimilarity between stand j and stand R_2
 D_{3j} = dissimilarity between stand j and stand R_3
 X_j = X-axis coordinate of stand j
 h_j = distance of stand j from X-axis
 h_{\max} = maximum distance of any stand from X-axis
 = distance of stand R_3 from X-axis
 = length of Y-axis
 Y_j = Y-axis coordinate of stand j
 X_{13} = X-axis coordinate of stand R_3

Steps in Construction:

1. Choose R_1 . Following Newsome and Dix (1968) I chose the stand which had the lowest sum of similarities with all other stands - Stand No.2.
2. Find R_2 and D_{12} . R_2 was chosen as the stand which was most dissimilar to R_1 (Stand 16). D_{12} was then the dissimilarity between Stands 2 and 16, equal to 98.2 units.

3. Calculate X-axis coordinates of all remaining stands, as measured from R_1 , using the equation:

$$X_j = \frac{(D_{1j})^2 + (D_{12})^2 - (D_{2j})^2}{2D_{12}}$$

4. Calculate the distance from the X-axis of all remaining stands and find h_{\max} and R_3 . These distances are calculated from the equation:

$$h_j = [(D_{1j})^2 - (X_j)^2]^{\frac{1}{2}}$$

The end stand of the Y-axis (R_3) was Stand 5 and h_{\max} , the Y-axis length, was 79.0 units.

5. Calculate the Y-axis coordinates of all remaining stands using the equation:

$$Y_j = \frac{(U_j)^2 + (h_{\max})^2 - (D_{3j})^2}{2h_{\max}}$$

where,

$$(U_j)^2 = (h_j)^2 + (X_j - X_{13})^2$$

APPENDIX B Cont'd.

<u>X - Y COORDINATES</u>		
	<u>X</u>	<u>Y</u>
1	58.7	34.6
2	0.0	0.0
3	48.2	41.1
4	66.7	51.0
5	51.8	79.0
6	24.5	22.2
7	46.8	47.5
8	50.8	66.3
9	59.1	60.2
10	63.0	62.1
11	49.3	28.0
12	63.5	58.2
13	63.3	15.6
14	54.5	69.4
15	51.2	47.5
16	98.2	0.0

APPENDIX C. List of Bryophytes

MOSSES

SPHAGNACEAE

Sphagnum fuscum (Schimp.) Klinggr.
Sphagnum warnstorffianum Du Rietz

FISSIDENTACEAE

Fissidens adianthoides Hedw.

DITRICHACEAE

Distichium capillaceum (Hedw.) B.S.G.
Distichium inclanatum (Hedw.) B.S.G.
Ditrichum flexicaule (Schwaegr.) Hamp.

DICRANACEAE

Dicranum bonjeani de Not. ex Lisa
Dicranum fuscens Turn.
Dicranum polysetum Sw.
Dicranum undulatum Brid.

POTTIACEAE

Tortella fragilis (Hook. and Wils.) Limpr.
Tortula ruralis (Hedw.) Gaertn., Meyer and Scherb.

SPLACHNACEAE

Tayloria lingulata (Dicks.) Lindb.
Tetraplodon angustatus (Hedw.) B.S.G.

BRYACEAE

Bryum creberrimum Tayl.
Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer and Scherb.
Bryum stenotrichum C. Mull.
Leptobryum pyriforme (Hedw.) Wils.

MNIACEAE

Mnium affine Bland. ex Funck
Mnium punctatum Hedw.
Mnium rostratum Schrad.

AULACOMNIACEAE

Aulacomnium palustre (Hedw.) Schwaegr.

MEESEACEAE

Meesea uliginosa Hedw.

THELEACEAE

Myurella julacea (Schwaegr.) G.S.G.

THUIDIACEAE

Abietinella agietina (Hedw.) Fleisch.

Thuidium recognitum (Hedw.) Lindb.

AMBLYSTEGIACEAE

Calliargon giganteum (Schimp.) Kindb.

Campylium stellatum (Hedw.) C. Jens.

Drepanocladus revolvens var. *intermedius* (Lindb. ex C. Hartm.)
Richs. and Wallace

Drepanocladus uncinatus (Hedw.) Warnst.

Drepanocladus vernicosus (Lindb. ex C. Hartm.) Warnst.

BRACHYTHECIACEAE

Brachythecium salebrosum (Web. and Mohr) B.S.G.

Tomenthypnum nitens (Hedw.) Loesek

ENTODONTACEAE

Pleurozium schreberi (Brid.) Mitt.

PLAGIOTHECIACEAE

Plagiothecium denticulatum (Hedw.) B.S.G.

HYPNACEAE

Ptilium crista-castrensis (Hedw.) De Not.

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) B.S.G.

POLYTRICHACEAE

Polytrichum juniperinum Hedw.

LIVERWORTS

PLAGIOCHILACEAE

Plagiochila asplenoides (L.) Dum.

LOPHOCOLEACEAE

Lophocolea minor Nees

RICCARDIACEAE

Riccardia pinguis (L.) S.F. Gray

LICHENS

Cladonia multiformis Merr.

Cladonia pyxidata (L.) Hoffm.

Cladonia cenotea (Ach.) Schaer.

Cladonia chlorophaea (Flörke) Spreng.

Cladonia arbuscula

Stereocaulon sp.

Peltigera apthosa (L.) Willd.

Peltigera apthosa var. *leucophlebia*

Peltigera canina var. *rufescens* (Weis.) Mudd.

APPENDIX D. List of Vascular Plant Species *

1. EQUISETACEAE

Equisetum arvense L.
Equisetum scirpoides Michx.
Equisetum variegatum Schleich.

2. PINACEAE

Abies lasiocarpa (Hook.) Nutt.
Juniperus communis L.
Juniperus horizontalis Moench 2, 9, 15
Picea engelmannii Parry
Picea glauca (Moench) Voss
Picea mariana (Mill.) B.S.P.
Pinus contorta Loudon var. *latifolia* Engelm.

3. JUNCAGINACEAE

Triglochin maritima L. 3

4. GRAMINEAE

Agropyron repens (L.) Beauv. 2
Agropyron trachycaulum (Link) Malte
Agrostis thurberiana Hitchc. 2
Bromus inermis Leyss. 2, 3
Bromus pumpellianus Scribn. 11
Calamagrostis canadensis (Michx.) Beauv.
Calamagrostis inexpansa A. Gray
Danthonia intermedia Vasey 2, 3, 6
Deschampsia caespitosa (L.) Beauv. 3, 6
Elymus innovatus Beal
Poa palustris L. 3, 4
Oryzopsis asperifolia Michx. 7

5. CYPERACEAE

Carex aquatilis Wahlenb.
Carex aurea Nutt.
Carex buxbaumii Wahlenb. 3, 7
Carex capillaris L.
Carex concinna R. Br.
Carex disperma Dewey 10
Carex eburnea Boott 5
Carex flava L.
Carex gynocrates Wormsk.
Carex interior Bailey 5, 9
Carex leptalea Wahlenb.
Carex rostrata Stokes
Carex scirpoidea Michx.
Carex vaginata Tausch
Eleocharis pauciflora (Lightf.) Link var. *fernaldii* Svenson
Eriophorum brachyantherum Trautv. 9
Scirpus pumilus Vahl.

6. JUNCACEAE

- Juncus alpinus* Vill. var. *rariflorus* Hartm. 6
Juncus balticus Willd.
Juncus tracyi Rydb. 7

7. LILIACEAE

- Lilium philadelphicum* L. var. *andinum* (Nutt.) Ker 2
Smilacina stellata (L.) Desf. 3, 5, 7
Tofieldia glutinosa (Michx.) Pers.
Tofieldia pusilla (Michx.) Pers. 6, 7, 9
Zygadenus elegans Pursh.

8. IRIDACEAE

- Sisyrinchium montanum* Greene 2, 6

9. ORCHIDACEAE

- Calypso bulbosa* (L.) Oakes 1
Habenaria dilatata (Pursh) Hook.
Habenaria obtusata (Pursh) Richards.
Habenaria viridis (L.) R.Br. var. *bracteata* (Muhl.) A. Gray
Listera cordata (L.) R.Br. 7, 16
Orchis rotundifolia Banks.

10. SALICACEAE

- Populus tremuloides* Michx.
Salix brachycarpa Nutt. 2
Salix candida Fluegge
Salix glauca L.
Salix mackenzieana (Hook.) Barratt
Salix myrtillofolia Anderss.
Salix vestita Pursh 9

11. BETULACEAE

- Alnus crispa* (Ait.) Pursh 15
Alnus tenuifolia Nutt. 4
Betula glandulosa Michx.

12. SANTALACEAE

- Geocaulon lividum* (Richards.) Fern.

13. POLYGONACEAE

- Polygonum viviparum* L.

14. RANUNCULACEAE

- Anemone multifida* Poir. 13
Anemone parviflora Michx.
Aquilegia flavescens S. Wats. 7, 15

15. SAXIFRAGACEAE

- Mitella nuda* L.
Parnassia fimbriata König 7
Parnassia montanensis Fern. & Rydb.
Parnassia palustris L. var. *neogaea* Fern. 3, 7
Parnassia parviflora DC. 6

16. ROSACEAE

- Dryas integrifolia* M. Vahl.
Fragaria virginiana Duchesne
Potentilla fruticosa L.
Rosa acicularis Lindl.
Rubus acaulis Michx.

17. LEGUMINOSAE

- Astragalus frigidus* (L.) A. Gray var. *americanus* (Hook.)
S. Wats.
Hedysarum alpinum L. 6, 11, 13

18. EMPETRACEAE

- Empetrum nigrum* L. 7, 9, 15

19. VIOLACEAE

- Viola renifolia* A. Gray

20. ELAEAGNACEAE

- Shepherdia canadensis* (L.) Nutt.

21. ONAGRACEAE

- Epilobium angustifolium* L.
Epilobium glandulosum Lehm. 3

22. UMBELLIFERAE

- Osmormiza* sp. 16

23. CORNACEAE

- Cornus canadensis* L.

24. PYROLACEAE

- Chimaphila umbellata* (L.) Bart. var. *occidentalis* (Rydb.)
Blake 16
Moneses uniflora (L.) A. Gray 1, 16
Pyrola asarifolia Michx.
Pyrola secunda L.

25. ERICACEAE

- Arctostaphylos rubra* (Rehder & Wils.) Fern.
Arctostaphylos uva-ursi (L.) Spreng.
Ledum groenlandicum Oeder

ERICACEAE cont'd.

- Oxycoccus microcarpus* Turcz.
Vaccinium caespitosum Michx.
Vaccinium scoparium Leiberg 7
Vaccinium vitis-idaea L. var. *Minus* Lodd.

26. PRIMULACEAE

- Dodecatheon radicum* Greene 2, 11
Primula egalikensis Wormskj. 6
Primula stricta Hornem. 6

27. GENTIANACEAE

- Gentianella amarella* (L.) Börner ssp. *acuta* (Michx.)
 J. M. Gillett 7, 11, 13

28. BORAGINACEAE

- Mertensia paniculata* (Ait.) G. Don

29. SCROPHULARIACEAE

- Castilleja septentrionalis* Lindl.
Pedicularis groenlandica Retz.
Pedicularis bracteosa Benth. 4, 7, 8

30. LENTIBULARIACEAE

- Pinguicula vulgaris* L. 4, 7, 9

31. RUBIACEAE

- Galium boreale* L.

32. CAPRIFOLIACEAE

- Linnaea borealis* L. var. *americana* (Forbes) Rehd.
Lonicera dioica L. var. *glaucescens* (Rydb.) Butters
Lonicera involucrata (Richards.) Banks 1, 15, 16

33. CAMPANULACEAE

- Campanula rotundifolia* L.

34. COMPOSITAE

- Achillea millefolium* L.
Agoseris glauca (Pursh) Raf. 13
Antennaria pulcherrima (Hook.) Greene
Arnica cordifolia Hook. 7, 13
Aster ciliolatus Lindl.
Aster sibiricus L. 6, 13
Erigeron acris L. var. *elatus* (Hook.) Cronq. 9
Erigeron glabellus Nutt. var. *pubescens* (Hook.) Cronq. 6
Petasites palmatus (Ait.) A. Gray
Petasites sagittatus (Pursh) A. Gray 3
Petasites vitifolius Greene 3

COMPOSITAE cont'd.

Senecio pauperculus Michx.
Solidago decumbens Greene
Solidago multiradiata Ait.

*The numbers following the names of some of the species indicate the stands in which these species were found. These species are not listed in Cover and Frequency Tables (Tables 7 and 8).

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